

# ZOOTAXA

4376

## Review of *Anaphes* Haliday (Hymenoptera: Mymaridae) with key to species in Europe and a world catalogue

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Magnolia Press  
Auckland, New Zealand

Accepted by G. Gibson: 8 Nov. 2017; published: 30 Jan. 2018

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(Zootaxa 4376)

104 pp.; 30 cm.

30 Jan. 2018

ISBN 978-1-77670-302-9 (paperback)

ISBN 978-1-77670-303-6 (Online edition)

FIRST PUBLISHED IN 2018 BY

Magnolia Press

P.O. Box 41-383

Auckland 1346

New Zealand

e-mail: magnolia@mapress.com

<http://www.mapress.com/j/zt>

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ISSN 1175-5326 (Print edition)

ISSN 1175-5334 (Online edition)

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## Abstract

The Walter Soyka species of *Anaphes* Haliday are reviewed and placed in context among the remaining world species. An analysis of his descriptions and identification keys is presented, and discussed in light of a broader interpretation of intraspecific variation in *Anaphes* species than Soyka accepted. An illustrated diagnosis of *Anaphes* is given and the species in Europe considered to be valid are keyed—14 species in *Anaphes (Anaphes)* and 15 species in *Anaphes (Patasson)*. The 244 names of world *Anaphes* are tabulated in various ways and their type localities, if known, are mapped. All available valid names and their synonyms, mostly from among the 155 nominal species described by Soyka, are catalogued, with details of type material and collecting information. A total of 167 synonyms are listed, 17 of which are synonyms proposed by earlier authors and 149 of which are proposed as new synonyms. Lectotypes are designated for *Mymar ferreirei* Soyka and *Yungaburra acutiventris* Soyka. Nine *nomina dubia*, 2 names of fossil species that most likely do not belong to *Anaphes*, 3 unavailable names and 20 species transferred to other genera are listed separately; among the latter, *Anagrus foersteri* (Ratzeburg) is transferred to *Erythmelus* Enock as *E. foersteri* (Ratzeburg), **comb. n.** Host records published from 1985–2015 are tabulated; most are from the literature but a few are from unpublished records found on slide mounted *Anaphes* specimens in various collections, mostly in Europe. The merits of classifying the available names of nominal species into an earlier classification with subgenera *Anaphes (Anaphes)* and *Anaphes (Patasson)* instead a later classification consisting of species groups within *Anaphes (Anaphes)* and *Anaphes (Yungaburra)* are discussed; the earlier classification is preferred.

**Key words:** Chalcidoidea, fairyfly, genus diagnosis, European species key, world lists, egg parasitoid

## Introduction

*Anaphes* Haliday (Hymenoptera: Mymaridae) is an apparently large genus containing about 235 nominal species of egg parasitoids, some of which have been used successfully in biological control against weevils (Coleoptera: Curculionidae) and leaf beetles (Coleoptera: Chrysomelidae). Debauche (1948) revised the Belgian *Anaphes* species and treated as subgenera *A. (Anaphes)* and *Anaphes (Patasson)*, originally described as genera by Haliday (1833) and Walker (1846), respectively. Ogloblin (1962) proposed *A. (Austranaphes)* for four species from southern Argentina, basing his subgenus on the 11-segmented male flagellum (apparently 10 segments in *Anaphes*, s. s., though Ogloblin did not state this). Graham (1982) discussed the name *Patasson* and designated lectotypes for six of the eight Haliday and Walker species; he failed to locate type material for two species. Huber (1992) reviewed the generic classification and also treated two subgenera, *A. (Anaphes)*, which includes almost all of the nominal species, and *Anaphes (Yungaburra* Girault). He classified the species of *A. (Anaphes)* in two species groups. One was the *fuscipennis* group (female clava 1-segmented), which included species described by Soyka in *Synanaphes* Soyka, *Mymar* Curtis [Soyka's name for *Anaphes*; Graham (1982)] considered it a misidentification), *Ferrierella* Soyka, and *Stammeriella* Soyka. The other was the *crassicornis* group (female clava 2-segmented), which included species described by Soyka and/or others as *Anaphoidea* Girault, *Antoniella* Soyka, *Fulmekiella* Soyka, *Hofenederia* Soyka, *Mariella* Soyka, and *Patasson*. *Anaphes (Yungaburra)* contained 10 nominal species classified in the *amplipennis* group (female clava entire), which included Ogloblin's *A. (Austranaphes)* species

from southern South America, and the *nitens* groups (female clava 2-segmented), which included several species from the Australian region. Huber (1992) redescribed and keyed the North American species of the *fuscipennis* species group and all the described species of *A. (Yungaburra)*, provided an alphabetical checklist of all nominal species of *Anaphes*, and listed species described originally in *Anaphes* but transferred to other genera. Huber (2006) reviewed and keyed the North American species of the *crassicornis* group. Huber (2009) described a species of *Anaphes* from Fiji. Huber & Triapitsyn (2017) described a remarkable *Anaphes* species from Republic of the Congo.

Schmiedeknecht (1909) catalogued 16 nominal species and placed them all in *Anaphes*, three of them, including the single non-European species mentioned, now belong correctly in other genera. He did not catalogue *Patasson*, with its only included species. Kryger (1950), in contrast, treated the species as belonging to two genera, *Anaphes* and *Patasson*; he did not catalogue the species. Both these papers are now of historical interest only.

*Anaphes* has 14 junior synonyms, the largest number of any genus of Mymaridae. Various authors have discussed and listed them, notably Annecke & Doutt (1961), who treated the names under 3 valid genera *Anaphes*, *Patasson*, and *Flabrinus* Rondani, the latter which they treated as unplaced. Graham (1982) and Huber (1992) discussed all the names. In strict chronological order the genus group names are: *Anaphes* Haliday 1833, *Patasson* Walker 1846, *Panthus* Walker 1846, *Flabrinus* Rondani 1877, *Anaphoidea* Girault 1909, *Clinomydar* Kieffer 1913, *Yungaburra* Girault 1933, *Synanaphes* Soyka 1946, *Ferrierella* Soyka 1946, *Hofenederia* Soyka 1946, *Fulmekiella* Soyka 1946, *Stammeriella* Soyka 1950, *Antoniella* Soyka 1950, *Mariella* Soyka 1950, and *Austranaphes* Oglöblin 1962. *Anaphoides* Enock (1915) is usually treated as a *nomen nudum* (Annecke & Doutt 1961; Huber 1992) but it may simply have been a *lapsus calami*; in any case it is an unavailable name. The name *Anaphidis* appears in the captions to figures in Rondani (1870), and is clearly a *lapsus calami* for *Anaphes*.

Triapitsyn (2010) gave an account of Walter Soyka's life, and discussed his collection of Mymaridae, collecting methods, habitats and localities. The great majority of *A. (Anaphes)* species were described from Europe, mainly by Soyka (1946a, 1946b, 1949, 1950, 1953a, 1953b, 1954, and 1955). Soyka's species concepts and, in particular his keys to species, do not account sufficiently for intraspecific variation, as already noted by Graham (1982: 204). Bakkendorf (1960) had previously realized that a better knowledge of intraspecific variability would fill in the gaps between forms described by Soyka as species. Because of Soyka's numerous new species descriptions, the list of nominal species of Mymaridae for Europe greatly exceeds the lists for any other biogeographical region, all of which have a larger and more diverse mymarid fauna, though not necessarily for *Anaphes* except perhaps in Australia and New Zealand. A few *Anaphes* species were described by several authors subsequent to Soyka but no attempt has been made to sort out Soyka's species. Here we provide the first review of European *Anaphes* species since Soyka last published on them over 60 years ago, in which we discuss/analyze his eight papers. We consider our work to be a clean-up operation in preparation for more detailed research on *Anaphes* taxonomy, both in Europe and elsewhere. A comprehensive revision that provides a more complete understanding of *Anaphes* species is well beyond the scope of this paper. In preparation for such a revision it would be wise to describe/redescribe the European species, especially any considered to be new, based on a series of specimens, e.g., at least 10 females and, if possible, 10 males, reared from identified hosts and suitably preserved for both morphological and molecular study. Minimally, DNA/RNA should be extracted using a non-destructive method (Polaszek *et al.* 2014) before slide mounting a specimen. Ribosomal RNA (28S D2 region), for example, is suitable for matching the sexes correctly.

## Methods

This study is based primarily on examination by one or both of us of most of the primary types of European *Anaphes* species. Many other specimens from various European museums were also examined and photographed by the junior author but are not treated here. They will be important to help elucidate species limits, especially because some of them were reared from known hosts, but the specimens are often not in very good condition for morphological study. Nevertheless, detailed study of these is needed and best done together with the remaining Soyka specimens (secondary types or non-types) and fresh material collected in a manner useful for DNA extraction before slide mounting and morphological study.

Most of the European types, including those of Soyka, and many other non-type specimens, had been

borrowed for study and photographed by the junior author using a Zenith Ultra 500 LT microscope and Nikon D7000 camera with Camera Control Pro 2 version 2.0 software, in preparation for our work on *Anaphes*. Occasionally only a paratype was photographed because the primary type was apparently unavailable for study, or was of the wrong sex (male) making useful comparison with other species almost impossible. Several paratypes of Soyka species, some Walker primary types, and primary types of two European species deposited in North American institutions were photographed in Ottawa. They were taken with a ProgRes C14<sup>plus</sup> digital camera attached to a Nikon Eclipse E800 compound microscope, and the resulting layers were combined electronically using Auto-Montage® or Zerene Stacker™ and the images enhanced as needed with Adobe® Photoshop (no retouching of primary types was done).

The senior author visited the junior author in Kőszeg, Hungary, for several days in 2010 to examine photographs taken by that time, concentrating on *Anaphes* (*Anaphes*) species [treated previously as the *fuscipennis* group of *A. (Anaphes)*]. This was followed immediately by a visit to the Natural History Museum in Vienna for three days to continue studying Soyka's primary types, particularly those of *Anaphes* (*Patasson*) species [treated previously as the *crassicornis* group of *A. (Anaphes)*]. Later, the junior author sent the images of primary types and a few other specimens to the senior author for further study. We more or less independently arrived at a list of likely synonyms among Soyka species and then discussed cases where the lists differed. We examined most of the primary types of other authors as well—those from outside of Europe by the senior author for his previous publications on *Anaphes* and those for Europe by both of us for the present paper.

Although there are still problems identifying and characterizing the non-Soyka species, it is the Soyka species that needed most attention. A detailed analysis of his *Anaphes* collection and publications is given below to provide the framework and perspective that helps explain his thinking, and also ours in order to justify the large number of synonyms we propose. The work of three other authors, H. Debauche, W. Hellén and G. Viggiani, is also commented on because they provided keys to some European species of *Anaphes*.

In order to make the genus more easily recognizable by non-specialists in Mymaridae an illustrated generic diagnosis is provided. We provide a key to the European species we recognize as valid. We tabulate in various ways all the nominal species of *Anaphes* to make it easier for future workers to find a species name. In the text and in Tables 4, 5 and 7 only the species epithet is given to avoid needless repetition of the genus (or genus abbreviation) and author and to make for smoother reading. The full scientific name (genus, species, author, date) for all *Anaphes* species is given in Tables 2, 3 and, especially, 6 where we summarize what we consider to be the valid species and their synonyms. We summarize host records separately (Table 7). Species names are given masculine endings regardless of the gender of the original generic names so as to conform to their correct current generic combination, i.e., *Anaphes*, which is masculine (Huber 1992, 2005, ICZN 2017).

Huber (2015a) described how to prepare suitable slide mounts of most Mymaridae. This is essential for the best chance of identifying a species correctly because only then can all the morphological features be seen. Unfortunately, permanent slide mounts means that characters only visible in lateral view cannot be studied if the specimen is mounted in dorsal view and *vice versa*. Good card mounts of fresh, critical point dried specimens are often very useful to describe habitus and colour. For *Anaphes*, colour is mostly of little use since most specimens are fairly uniformly black or dark brown, but the shape of the gaster in lateral view and dorsal view is often useful to help characterize a species though it is difficult to describe. Wings should be removed and mounted separately before the body is cleared. When slide mounting *Anaphes* specimens, it is important to mount a cleared specimen with the head face up, as in Figs 32 and 52 (with or without antennae still attached, spread away from the face and horizontal), and preferably under its own coverslip. If the head is not detached from the body and is mounted in lateral view with antenna still attached, e.g. Figs 34, 35, it can still be used for accurate measurements of antennal segments but the supraorbital suture extension cannot easily be seen—this must be observed to make the correct choice in couple 2 of the key. In contrast, the cleared mesosoma + metasoma should be mounted laterally under a second coverslip, e.g. Fig. 56, so ovipositor length (or, sometimes more easily, an ovipositor sheath measured from anterior apex of basal loop of ovipositor to apex of sheath), metatibia length, and lengths of metatarsomeres 1 and 2 can be accurately measured and some idea obtained of how far the ovipositor (within the basal sac of the gaster) extends anteriorly under the mesosoma. Minimally, at least two females of a morphospecies should be slide mounted, one with mesosoma (with or without the metasoma) in dorsal view, so as to be able to examine the mesosomal sculpture, and one in lateral view. Because it is very difficult to position the metasoma in dorsal view it may be necessary to detach it from the mesosoma and mount it laterally.

Abbreviations for morphological terms used in the keys are: fl = funicle segment; mps = multiporous plate sensilla (= longitudinal sensilla, of authors); abbreviations used on the figures are listed in Table 8. Arnold Förster spelled his name in two different ways (Förster and Foerster) in his various publications. In the references and for the author of the species we used the spelling given in the original publication; otherwise we use the current German spelling, with a dieresis over the “o”.

Primary types of *Anaphes* are deposited in 20 institutions. A few other institutions that have slide or card mounted *Anaphes* (among other Mymaridae) and the two nominal species represented by fossils in amber are also listed below. Their acronyms (codens) and those for some institutions with non-type specimens mostly follow Evenhuis (2014) but with the institution named first and country last.

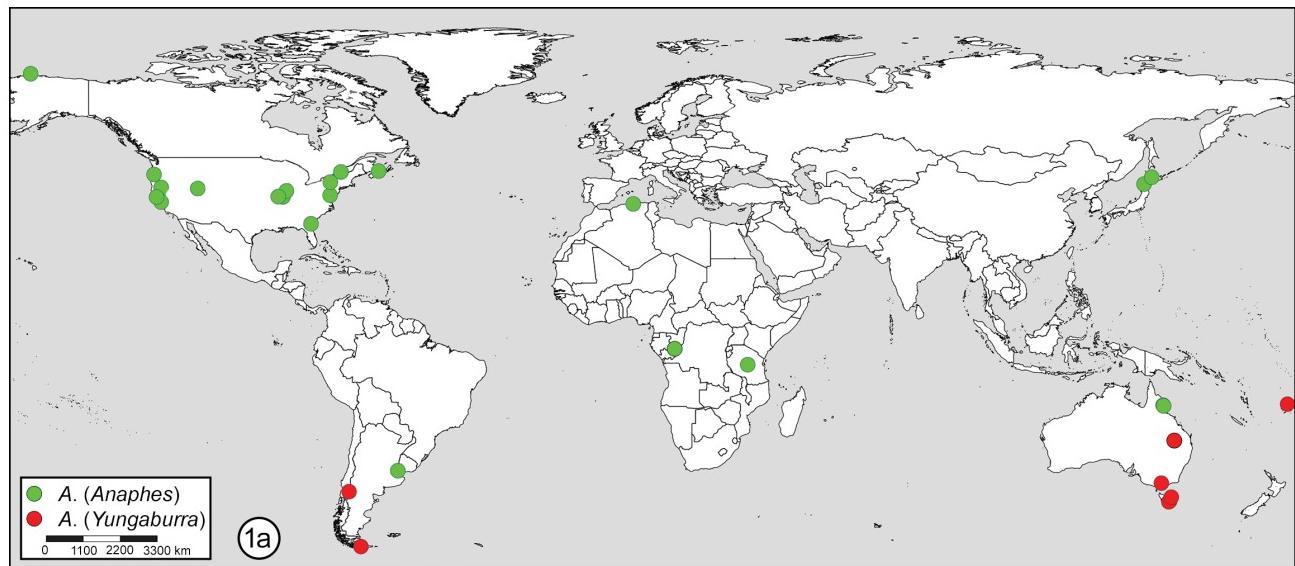
ANIC	Australian National Insect Collection, Canberra, Australian Capital Territory, Australia.
BMNH	Natural History Museum, London, England.
BPBM	Bernice P. Bishop Museum, Honolulu, Hawaii, USA.
CAS	California Academy of Sciences, San Francisco, California, USA.
CNC	Canadian National Collection of Insects, Arachnids and Nematodes, Ottawa, Ontario, Canada.
CUIC	Cornell University, Ithaca, New York, USA.
DEI	Senckenberg Deutsches Entomologisches Institut. Müncheberg, Germany.
DEZA	Dipartimento di Entomologia e Zoologia Agraria dell’Università degli Studi di Napoli «Frederico II», Portici, Naples, Italy.
EMEC	Essig Museum of Entomology, University of California, Berkeley, California, USA.
INHS	Illinois Natural History Survey, Champaign, Illinois, USA.
IRSNB	Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium.
MACN	Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires, Argentina.
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA.
MHNG	Muséum d’Histoire Naturelle, Geneva, Switzerland.
MVMA	Museum of Victoria, Melbourne, Victoria, Australia.
MZUF	Museo Zoologico “La Specola”, Florence, Italy.
NHMW	Naturhistorisches Museum, Vienna, Austria.
NIAES	National Institute for Agro-Environmental Sciences, Tsukuba, Japan.
NMID	National Museum of Ireland, Dublin, Ireland.
QM	Queensland Museum, South Brisbane, Queensland, Australia.
USNM	National Museum of Natural History, Washington, District of Columbia, USA.
ZMHB	Museum für Naturkunde der Humboldt-Universität, Berlin, Germany.
ZMSP	Russian Academy of Sciences, Zoological Institute, Saint Petersburg, Russia.
ZMUC	University of Copenhagen Zoological Museum, Copenhagen, Denmark.

## Results

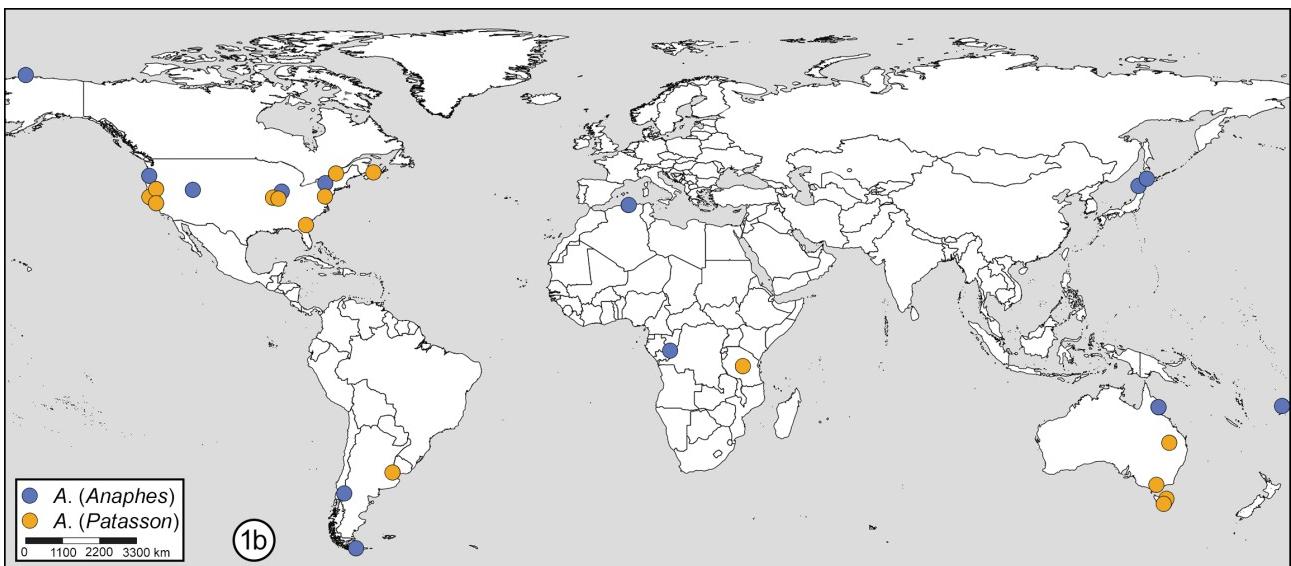
Soyka described The majority of the world’s 236 nominal species (including 1 subspecies) of *Anaphes*. Other authors described 79 nominal species, just over one-third of the total. In descending order by number of species described (alphabetically by author if only one species described) they are: Soyka 155, Girault 18, Debauche 14, Huber 9 (including two with Prinsloo and one with Triapitsyn), Walker 7, Förster 6, Doutt 5 (including one with Annecke), Ogloblin 4, Mathot 3, Jesu 2, Ashmead 1, Bakkendorf 1, Bojoc 1, Brèthes 1, Crosby & Leonard 1, Ferrière 1, Gahan 1, Ghidini 1, Haliday 1, Kieffer 1, Kuwayama 1, and Rondani 1. These numbers include 9 *nomina dubia* but exclude 3 unavailable names, 3 replacement names and 2 names of fossil species that almost certainly are misclassified in *Anaphes*.

Tables 1–6 summarize information on the nominal species of *Anaphes*. Table 1 is an alphabetical list of the world nominal species, updated and corrected from the list given in Huber (1992) but using the original spelling of all the included species names. Excluding 3 replacement names, a total of 231 available names are correctly assigned to *Anaphes* (names doubtfully or incorrectly assigned to *Anaphes* are at the end of Table 6; 2 are fossil species and 20 belong in other genera). Table 2 is a strictly chronological list (by year, page, and location on page)

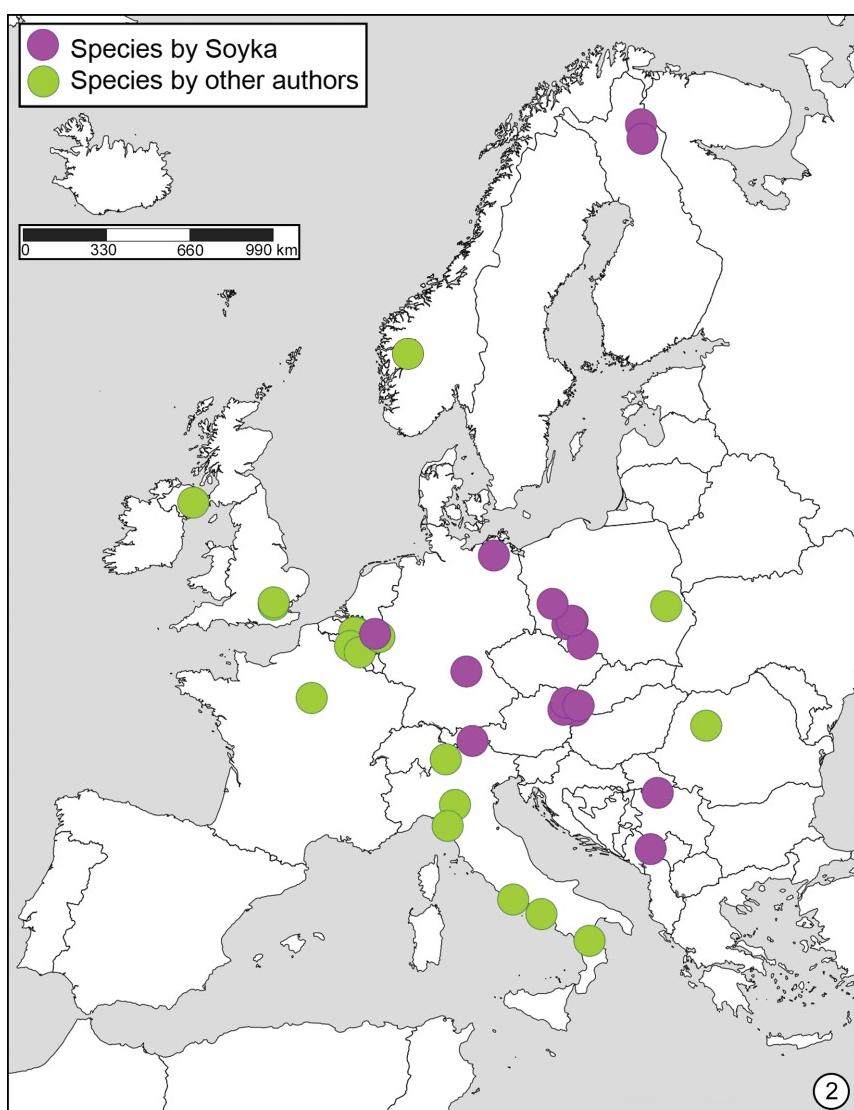
of the world nominal species. Sixteen nominal species were described in the 1800s, 211 in the 1900s, and 4 so far in the 2000s. In Table 3 we again list chronologically the available names but organize them by species in *A. (Anaphes)* followed by species in *A. (Patasson)*. To put Soyka's species in context geographically, we list in two different ways (Tables 4 and 5) all the geo-referenced collecting localities for primary type specimens of world species—in Table 4 each locality is followed by an alphabetical list of nominal species, whereas in Table 5 each locality is followed by a chronological list of nominal species within each subgenus. In addition, all the primary type localities are mapped for the world excluding Europe (Figs 1a, 1b), and for Europe (Fig. 2). Geographical coordinates were found using Google Earth and are given to the nearest minute. Occasionally, the locality as found on Google Earth did not match the co-ordinates as given on the type slide, e.g., *fennicus* [the paratype slide may actually be the holotype that Soyka mislabelled] or the published type locality referred to two places, e.g., *tarsalis* and *wolfsthalii*. It must not be assumed that a type specimen actually came from the exact coordinates given. For example, Soyka's species described from Hundsheim (Austria) came from hay brought to his house from the surrounding fields and stored in a room with a large window at the back of the house, as explained and illustrated by Triapitsyn (2010). Mymaridae emerging from the hay were collected from the window panes and described as being from Hundsheim. Soyka also collected many specimens from a window or windows of St. Ignatius College [written as “Ignatiuskolleg” on the holotype slides] in Valkenburg (The Netherlands) and from a locality (farm?) called Jettchenhof, about 2.5 km north of Malchin (Germany) so the type locality could be narrowed down to a particular building though of course the specimens may have drifted or been blown in from some distance away. Huber (1992) identified five specimens (in USNM) from Ithaca, New York, USA of *fuscipennis* that had been extracted from the stomach of a trout, indicating that the specimens had blown out onto a body of water, possibly quite far from land. This is additional evidence that specimens of *Anaphes* (and other Mymaridae) get blown around and may land in areas obviously unsuitable for survival and reproduction. Table 6 contains the main results of the present study—a list of senior synonyms and all their junior synonyms, followed by details of the collecting event as recorded in the original descriptions, with French and German words translated as needed. The 10 nominal species in *A. (Yungaburra)* are reclassified into *A. (Anaphes)* or *A. (Patasson)* in Tables 3 and 6 because a classification of *Anaphes* into *A. (Anaphes)* with two included species groups, and *A. (Yungaburra)* is best abandoned, as discussed below.



**FIGURE 1a.** World (excluding European) type localities of *Anaphes (Anaphes)* and *A. (Yungaburra)*; classification according to Huber (1992). See Tables 4 and 5 for localities.



**FIGURE 1b.** World (excluding European) type localities of *Anaphes* (*Anaphes*) and *A. (Patasson)*; classification according to Debauche (1949) and the present paper. See Tables 4 and 5 for localities.



**FIGURE 2.** European type localities of *Anaphes* (*Anaphes*). See Tables 4 and 5 for localities.

**TABLE 1.** Nominal species with original spellings, listed alphabetically. See Tables 2 or 6 for spellings that agree in gender with *Anaphes* (in which all the species listed are now classified), which is masculine. The list has 244 names of which 236 (including 9 *nomina dubia*) are available nominal species. Details on the *nomina dubia*, the 3 replacement names, the 3 unavailable names, and the 2 names of fossil species that are almost certainly not *Anaphes* but are provisionally retained there for lack of somewhere more suitable to place them are given in Table 6. Species transferred to other genera are also listed there.

<i>acutipennis</i> Soyka, 1949	
<i>acutiventris</i> Soyka, 1949	
<i>addita</i> Soyka, 1949	
<i>aequipennata</i> Soyka, 1953	
<i>aequa</i> Soyka, 1953	
<i>aestiva</i> Soyka, 1950	
<i>alaskae</i> Annecke & Doutt, 1961	
<i>albipes</i> Soyka, 1949	
<i>amplipennis</i> Ogloblin, 1962	
<i>angustipennis</i> Debauche, 1948	
<i>angustipennis</i> Soyka, 1949	
<i>antoniae</i> Soyka, 1955	
<i>apilosa</i> Soyka, 1949	
<i>archettii</i> Ghidini, 1945	
<i>arcuata</i> Soyka, 1953	
<i>arenbergi</i> Debauche, 1948	
<i>aries</i> Debauche, 1948	
<i>aterrima</i> Soyka, 1949	
<i>atomarius</i> Brèthes, 1913	
<i>atra</i> Soyka, 1949	
<i>auripes</i> Walker, 1846	
<i>australia</i> Girault, 1920	
<i>autumnalis</i> Foerster, 1847	
<i>avalae</i> Soyka, 1955	
<i>balteata</i> Soyka, 1949	
<i>basalis</i> Förster, 1861	
<i>behmani</i> Girault, 1929	
<i>bicolor</i> Soyka, 1953	
<i>brachygaster</i> Debauche, 1948	
<i>brevicornis</i> Soyka, 1949	
<i>brevior</i> Soyka, 1949	
<i>brevis</i> Walker, 1846	
<i>brevitarsis</i> Soyka, 1949	
<i>breviventris</i> Soyka, 1949	
<i>brunnea</i> Doutt, 1949	
<i>byrrhidiphagus</i> Huber, 1992	
<i>calendrae</i> Gahan, 1927	
<i>calvescens</i> Debauche, 1948	
<i>campestris</i> Soyka, 1949	
<i>capitulata</i> Soyka, 1949	
<i>chrysomelae</i> Bakkendorf, 1960	
<i>ciliatus</i> Soyka, 1949	
<i>cincta</i> Soyka, 1949	
<i>collinus</i> Walker, 1846	
<i>communis</i> Soyka, 1949	
<i>comosipennis</i> Girault, 1917	
<i>compressus</i> Soyka, 1949	
<i>conferta</i> Doutt, 1949	
<i>congener</i> Förster, 1861	
<i>conotracheli</i> Girault, 1905	
<i>consimilis</i> Soyka, 1949	
	<i>cotei</i> Huber, 1997
	<i>crassicornis</i> Walker, 1846
	<i>crassicornis</i> Soyka, 1949
	<i>crassipennis</i> Soyka, 1946
	<i>crassipilis</i> Soyka, 1949
	<i>crassa</i> Soyka, 1953
	<i>cultripennis</i> Debauche, 1948
	<i>debilipennis</i> Soyka, 1949
	<i>declinata</i> Soyka, 1950
	<i>depressa</i> Soyka, 1954
	<i>dessarti</i> Mathot, 1969
	<i>devillei</i> Debauche, 1948
	<i>devia</i> Soyka, 1949
	<i>diana</i> Girault, 1911
	<i>differens</i> Soyka, 1949
	<i>dilatata</i> Soyka, 1949
	<i>discolor</i> Soyka, 1949
	<i>discolorsimilis</i> Soyka, 1950
	<i>distincta</i> Soyka, 1953
	<i>dorcas</i> Debauche, 1948
	<i>dubia</i> Soyka, 1949
	<i>duplicata</i> Soyka, 195.
	<i>dytiscidarum</i> Rimsky-Korsakov, 1920
	<i>elegans</i> Soyka, 1955
	<i>elongata</i> Soyka, 1949
	<i>ensipennis</i> Soyka, 1949
	<i>curyale</i> Debauche, 1948
	<i>exiguosimilis</i> Soyka, 1953
	<i>exigua</i> Soyka, 1949
	<i>eulongicornis</i> Özdikmen, 2011
	<i>fabarius</i> Rondani, 1877
	<i>falsa</i> Soyka, 1953
	<i>fennicus</i> Soyka, 1955
	<i>ferrierei</i> Soyka, 1946
	<i>fijiensis</i> Huber, 2009
	<i>filicornis</i> Soyka, 1949
	<i>flavicornis</i> Soyka, 1949
	<i>flavipes</i> Förster, 1841
	<i>flavitaris</i> Soyka, 1949
	<i>flavus</i> Soyka, 1949
	<i>fortipennis</i> Soyka, 1953
	<i>fuscipennis</i> Haliday, 1833
	<i>gabitzi</i> Soyka, 1953
	<i>galtoni</i> Girault, 1912
	<i>gauthieri</i> Debauche, 1948
	<i>germaniacus</i> Özdikmen, 2011
	<i>gerrisophaga</i> Doutt, 1949
	<i>globosicornis</i> Soyka, 1949
	<i>globosa</i> Soyka, 1949
	<i>gonipteri</i> Ferrière, 1930
	<i>gracilior</i> Soyka, 1949

.....continued on the next page

**TABLE1.** (continued)

<i>gracillimus</i> Soyka, 1955	<i>nitens</i> Girault, 1928
<i>hercules</i> Girault, 1911	<i>nunezi</i> Ogloblin, 1962
<i>heterotomus</i> Mathot, 1969	<i>obscura</i> Soyka, 1949
<i>hundsheimensis</i> Soyka, 1946	<i>obsoleta</i> Soyka, 1954
<i>inexpectatus</i> Huber & Prinsloo, 1990	<i>ordinaria</i> Soyka, 1954
<i>intermedia</i> Soyka, 1949	<i>ornata</i> Soyka, 1949
<i>iole</i> Girault, 1911	<i>ovata</i> Soyka, 1949
<i>iole anomocerus</i> Girault, 1929	<i>ovijentatus</i> Crosby & Leonard, 1914
<i>kressbachi</i> Soyka, 1949	<i>ovipositor</i> Soyka, 1946
<i>lacensis</i> Soyka, 1949	<i>pallida</i> Soyka, 1949
<i>lameerei</i> Debauche, 1948	<i>pallidicornis</i> Soyka, 1949
<i>laticornis</i> Soyka, 1949	<i>pallidipes</i> Soyka, 1949
<i>latipennis</i> Walker, 1846	<i>palliditarsis</i> Soyka, 1949
<i>latipterus</i> Bočoc, 1962	<i>pallipes</i> Ashmead, 1887
<i>lata</i> Soyka, 1949	<i>pannonica</i> Soyka, 1946
<i>lemae</i> Bakkendorf, 1970	<i>parallelipennis</i> Soyka, 1949
<i>leonhardwitzi</i> Soyka, 1949	<i>parciventris</i> Soyka, 1949
<i>leptoceras</i> Debauche, 1948	<i>parvus</i> Förster, 1841
<i>linearis</i> Soyka, 1949	<i>pectoralis</i> Soyka, 1946
<i>lineipennis</i> Soyka, 1949	<i>pellucens</i> Soyka, 1949
<i>linnaei</i> Girault, 1912	<i>perdubius</i> Girault, 1916
<i>listronoti</i> Huber, 1997	<i>peyerimhoffi</i> Kieffer, 1913
<i>longiclava</i> Doutt, 1949	<i>piceicornis</i> Soyka, 1954
<i>longicornis</i> Walker, 1846	<i>pilicornis</i> Soyka, 1949
<i>longicornis</i> Soyka, 1949	<i>piliscapus</i> Soyka, 1949
<i>longior</i> Soyka, 1949	<i>pilosipennis</i> Soyka, 1949
<i>longipennis</i> Soyka, 1949	<i>pilosissima</i> Soyka, 1954
<i>longipilis</i> Soyka, 1954	<i>pinguicornis</i> Soyka, 1949
<i>longispinosus</i> Soyka, 1955	<i>pratensis</i> Förster, 1847
<i>lucida</i> Soyka, 1949	<i>pucarobius</i> Ogloblin, 1962
<i>luna</i> Girault, 1914	<i>pulcher</i> Soyka, 1949
<i>luteicornis</i> Soyka, 1955	<i>pulchripennis</i> Soyka, 1949
<i>maculata</i> Soyka, 1949	<i>pullicrurus</i> Girault, 1910
<i>maculicornis</i> Soyka, 1949	<i>quadraticornis</i> Soyka, 1949
<i>maialis</i> Debauche, 1948	<i>quinquearticulatus</i> Huber & Triapitsyn, 2017
<i>malchinensis</i> Soyka, 1949	<i>ranalteri</i> Soyka, 1946
<i>malkwitzi</i> Soyka, 1949	<i>rectipennis</i> Soyka, 1949
<i>maradonae</i> Jesu, 2003	<i>reducta</i> Soyka, 1949
<i>medioacuta</i> Soyka, 1954	<i>regulus</i> Walker, 1846
<i>medius</i> Soyka, 1946	<i>relicta</i> Soyka, 1949
<i>minima</i> Soyka, 1949	<i>rotundipennis</i> Soyka, 1949
<i>minor</i> Soyka, 1949	<i>rufa</i> Soyka, 1949
<i>mirabilis</i> Soyka, 1955	<i>saintpierrei</i> Girault, 1913
<i>nemorosa</i> Soyka, 1954	<i>schellwieniens</i> Meunier, 1901
<i>neobrevior</i> Soyka, 1954	<i>semiflava</i> Soyka, 1949
<i>neodistincta</i> Soyka, 1954	<i>semimedia</i> Soyka, 1949
<i>neoflava</i> Soyka, 1949	<i>serbica</i> Soyka, 1949
<i>neopratensis</i> Soyka, 1946	<i>serenus</i> Soyka, 1955
<i>neoserenus</i> Soyka, 1955	<i>sibbei</i> Soyka, 1954
<i>neospecialis</i> Soyka, 1955	<i>siegerfeldi</i> Soyka, 1955
<i>neuquenensis</i> Ogloblin, 1962	<i>silesica</i> Soyka, 1946a
<i>neustadtii</i> Soyka, 1949	<i>similis</i> Soyka, 1949
<i>nigerrima</i> Soyka, 1949	<i>sinipennis</i> Girault, 1911
<i>nigra</i> Soyka, 1949	<i>sordidata</i> Girault, 1909
<i>nigrellus</i> Girault, 1911	<i>soykai</i> Özdi̇kmen, 2011
<i>nigricornis</i> Soyka, 1949	<i>specialis</i> Soyka, 1955
<i>nigroparva</i> Soyka, 1954	<i>speciosior</i> Soyka, 1954
<i>nipponicus</i> Kuwayama, 1932	<i>speciosus</i> Soyka, 1955

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**TABLE1.** (continued)

<i>spinosus</i> Soyka, 1949	<i>thoracicus</i> Soyka, 1955
<i>splendens</i> Meunier, 1901	<i>timida</i> Soyka, 1950
<i>stammeri</i> Soyka, 1949	<i>trijohanni</i> Jesu, 2002
<i>stratipennis</i> Soyka, 1954	<i>valkenburgica</i> Soyka, 1949
<i>stubaensis</i> Soyka, 1949	<i>variata</i> Soyka, 1949
<i>stygius</i> Debauche, 1948	<i>varicolor</i> Soyka, 1949
<i>sulphuripes</i> Soyka, 1949	<i>victus</i> Huber, 1997
<i>superaddita</i> Soyka, 1950	<i>vulgaris</i> Soyka, 1946
<i>swiedecki</i> Soyka, 1953	<i>vulgarisimilis</i> Soyka, 1954
<i>tarsalis</i> Mathot, 1969	<i>weidenhofti</i> Soyka, 1954
<i>tasmaniae</i> Huber & Prinsloo, 1990	<i>wertaneki</i> Soyka, 1955
<i>tenuipennis</i> Soyka, 1949	<i>wolfsthalii</i> Soyka, 1950
<i>tenuis</i> Soyka, 1949	<i>wratislawensis</i> Soyka, 1954

**TABLE 2.** Available names of nominal species of *Anaphes* listed strictly chronologically, i.e., by year, by month (if same year), by page (if same publication) and by order of description on page (if on same page). The original genus is given in parenthesis. The 40 non-European species are listed with country in bold. Species placed by Huber (1992) in *Anaphes* (*Yungaburra*) are identified by an asterisk (\*). The two fossils species, *splendens* Meunier, 1901 and *schellwieniens* Meunier, 1901, are almost certainly not *Anaphes*; they are not listed here but are listed in Table 1 and discussed in Table 6.

<i>fuscipennis</i> Haliday, 1833: 346 ( <i>Anaphes</i> )
<i>flavipes</i> (Förster, 1841: 43) ( <i>Gonatocerus</i> )
<i>parvus</i> (Förster, 1841: 43) ( <i>Gonatocerus</i> )
<i>collinus</i> Walker, 1846: 52 ( <i>Anaphes</i> )
<i>longicornis</i> Walker, 1846: 52 ( <i>Anaphes</i> )
<i>regulus</i> Walker, 1846: 52 ( <i>Anaphes</i> )
<i>auripes</i> Walker, 1846: 52 ( <i>Anaphes</i> )
<i>brevis</i> Walker, 1846: 52 ( <i>Anaphes</i> )
<i>latipennis</i> Walker, 1846: 52 ( <i>Anaphes</i> )
<i>crassicornis</i> (Walker, 1846: viii [Errata and addenda]) ( <i>Patasson</i> )
<i>pratensis</i> Foerster, 1847: 211 ( <i>Anaphes</i> )
<i>autumnalis</i> Foerster, 1847: 212 ( <i>Anaphes</i> )
<i>congener</i> Förster, 1861: 42 ( <i>Anaphes</i> )
<i>basalis</i> Förster, 1861: 42 ( <i>Anaphes</i> )
<i>fabarius</i> (Rondani, 1877: 180) ( <i>Flabrimus</i> )
<i>pallipes</i> (Ashmead, 1887: 193) ( <i>Alaptus</i> ) <b>USA</b>
<i>conotrachelii</i> Girault, 1905: 220 ( <i>Anaphes</i> ) <b>USA</b>
<i>sordidatus</i> (Girault, 1909: 169) ( <i>Anaphoidea</i> ) <b>USA</b>
<i>pullicrurus</i> (Girault, 1910: 252) ( <i>Anaphoidea</i> ) <b>USA</b>
<i>diana</i> (Girault, 1911a: 215) ( <i>Anaphoidea</i> )
<i>sinipennis</i> Girault, 1911b: 280 ( <i>Anaphes</i> ) <b>USA</b>
<i>nigrellus</i> Girault, 1911b: 282 ( <i>Anaphes</i> ) <b>USA</b>
<i>iole</i> Girault, 1911b: 284 ( <i>Anaphes</i> ) <b>USA</b>
<i>hercules</i> Girault, 1911b: 285 ( <i>Anaphes</i> ) <b>USA</b>
* <i>galtoni</i> (Girault, 1912: 152) ( <i>Anaphoidea</i> ) <b>Australia</b>
<i>linnaei</i> (Girault, 1912: 153) ( <i>Anaphoidea</i> ) <b>Australia</b>
<i>atomarius</i> (Brèthes, 1913: 100) ( <i>Anaphoidea</i> ) <b>Argentina</b>
<i>peyerimhoffi</i> (Kieffer, 1913: 101) ( <i>Clinomymar</i> ) <b>Algeria</b>
<i>saintpierrei</i> Girault, 1913: 117 ( <i>Anaphes</i> ) <b>Australia</b>
<i>ovijentatus</i> (Crosby & Leonard, 1914: 181) ( <i>Anagrus</i> ) <b>USA</b>
<i>luna</i> (Girault, 1914b: 109) ( <i>Anaphoidea</i> )
<i>perdubius</i> Girault, 1916: 6 ( <i>Anaphes</i> ) <b>USA</b> .
<i>comosipennis</i> Girault, 1917: 17 ( <i>Anaphes</i> ) <b>Tanzania</b>
<i>australia</i> (Girault, 1920: 97) ( <i>Anaphoidea</i> ) <b>Australia</b>

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**TABLE 2.** (Continued)

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<i>calendrae</i> (Gahan, 1927: 32) ( <i>Anaphoidea</i> ) <b>USA</b>
* <i>nitens</i> (Girault, 1928: 262) ( <i>Anaphoidea</i> ) <b>Australia</b>
<i>iole anomocerus</i> Girault, 1929: 13 ( <i>Anaphes</i> ) <b>USA</b>
<i>behmani</i> Girault, 1929: 14 ( <i>Anaphes</i> ) <b>USA</b>
* <i>gonipteri</i> (Ferrière, 1930: 38) ( <i>Anaphoidea</i> ) <b>Australia</b>
<i>nipponicus</i> Kuwayama, 1932: 93 ( <i>Anaphes</i> ) <b>Japan</b>
<i>archetti</i> Ghidini, 1945: 39 ( <i>Anaphes</i> )
<i>medius</i> (Soyka, 1946a: 40) ( <i>Synanaphes</i> )
<i>crassipennis</i> (Soyka, 1946a: 41) ( <i>Mymar</i> )
<i>ovipositor</i> (Soyka, 1946a: 41) ( <i>Ferrierella</i> )
<i>silesicus</i> (Soyka, 1946a: 42) ( <i>Anaphoidea</i> )
<i>vulgaris</i> (Soyka, 1946a: 42) ( <i>Anaphoidea</i> )
<i>pannonicus</i> (Soyka, 1946a: 42) ( <i>Anaphoidea</i> )
<i>ferrierei</i> (Soyka, 1946b: 180) ( <i>Mymar</i> )
<i>ranalteri</i> (Soyka, 1946b: 181) ( <i>Synanaphes</i> )
<i>neopratensis</i> (Soyka, 1946b: 182) ( <i>Ferrierella</i> )
<i>pectoralis</i> (Soyka, 1946b: 183) ( <i>Hofenederia</i> )
<i>hundsheimensis</i> (Soyka, 1946b: 184) ( <i>Fulmekiella</i> )
<i>cultripennis</i> Debauche, 1948: 162 <i>Anaphes</i> ( <i>Anaphes</i> )
<i>stygius</i> Debauche, 1948: 165 <i>Anaphes</i> ( <i>Anaphes</i> )
<i>arenbergi</i> Debauche, 1948: 166 <i>Anaphes</i> ( <i>Anaphes</i> )
<i>aries</i> Debauche, 1948: 168 <i>Anaphes</i> ( <i>Anaphes</i> )
<i>gauthieri</i> Debauche, 1948: 171 <i>Anaphes</i> ( <i>Anaphes</i> )
<i>uryale</i> Debauche, 1948: 174 <i>Anaphes</i> ( <i>Patasson</i> )
<i>brachygaster</i> Debauche, 1948: 176 <i>Anaphes</i> ( <i>Patasson</i> )
<i>devillei</i> Debauche, 1948: 177 <i>Anaphes</i> ( <i>Patasson</i> )
<i>dorcas</i> Debauche, 1948: 179 <i>Anaphes</i> ( <i>Patasson</i> )
<i>calvescens</i> Debauche, 1948: 180 <i>Anaphes</i> ( <i>Patasson</i> )
<i>lameerei</i> Debauche, 1948: 182 <i>Anaphes</i> ( <i>Patasson</i> )
<i>angustipennis</i> Debauche, 1948: 184 <i>Anaphes</i> ( <i>Patasson</i> )
<i>maialis</i> Debauche, 1948: 185 <i>Anaphes</i> ( <i>Patasson</i> )
<i>leptoceras</i> Debauche, 1948: 187 <i>Anaphes</i> ( <i>Patasson</i> )
<i>pulcher</i> (Soyka, 1949: 312) ( <i>Mymar</i> )
<i>acutipennis</i> (Soyka, 1949: 315) ( <i>Mymar</i> )
<i>brevicornis</i> (Soyka, 1949: 316) ( <i>Mymar</i> )
<i>ciliatus</i> (Soyka, 1949: 317) ( <i>Mymar</i> )
<i>crassicornis</i> (Soyka, 1949: 318) ( <i>Mymar</i> )
<i>ensipennis</i> (Soyka, 1949: 320) ( <i>Mymar</i> )
<i>flavus</i> (Soyka, 1949: 321) ( <i>Mymar</i> )
<i>globosicornis</i> (Soyka, 1949: 322) ( <i>Mymar</i> )
<i>gracilior</i> (Soyka, 1949: 323) ( <i>Mymar</i> )
<i>leonhardwitzi</i> (Soyka, 1949: 324) ( <i>Mymar</i> )
<i>nigricornis</i> (Soyka, 1949: 325) ( <i>Mymar</i> )
<i>pilicornis</i> (Soyka, 1949: 326) ( <i>Mymar</i> )
<i>piliscapus</i> (Soyka, 1949: 327) ( <i>Mymar</i> )
<i>pilosipennis</i> (Soyka, 1949: 328) ( <i>Mymar</i> )
<i>quadraticornis</i> (Soyka, 1949: 329) ( <i>Mymar</i> )
<i>spinosus</i> (Soyka, 1949: 330) ( <i>Mymar</i> )
<i>sulphuripes</i> (Soyka, 1949: 330) ( <i>Mymar</i> )
<i>lacensis</i> (Soyka, 1949: 335) ( <i>Synanaphes</i> )
<i>angustipennis</i> (Soyka, 1949: 339) ( <i>Ferrierella</i> )
<i>brevitarsis</i> (Soyka, 1949: 340) ( <i>Ferrierella</i> )
<i>breviventris</i> (Soyka, 1949: 341) ( <i>Ferrierella</i> )
<i>capitulatus</i> (Soyka, 1949: 341) ( <i>Ferrierella</i> )
<i>dilatatus</i> (Soyka, 1949: 342) ( <i>Ferrierella</i> )
<i>filicornis</i> (Soyka, 1949: 343) ( <i>Ferrierella</i> )
<i>intermedius</i> (Soyka: 1949: 344) ( <i>Ferrierella</i> )

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**TABLE 2.** (Continued)

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<i>laticornis</i> (Soyka, 1949: 345) ( <i>Ferrierella</i> )
<i>maculatus</i> (Soyka, 1949: 345) ( <i>Ferrierella</i> )
<i>pulchripennis</i> (Soyka, 1949: 348) ( <i>Ferrierella</i> )
<i>stammeri</i> (Soyka, 1949: 349) ( <i>Ferrierella</i> )
<i>tenuipennis</i> (Soyka, 1949: 350) ( <i>Ferrierella</i> )
<i>varicolor</i> (Soyka, 1949: 350) ( <i>Ferrierella</i> )
<i>additus</i> (Soyka, 1949: 354) ( <i>Anaphoidea</i> )
<i>albipes</i> (Soyka, 1949: 355) ( <i>Anaphoidea</i> )
<i>apiulosus</i> (Soyka, 1949: 356) ( <i>Anaphoidea</i> )
<i>brevior</i> (Soyka, 1949: 357) ( <i>Anaphoidea</i> )
<i>communis</i> (Soyka, 1949: 358) ( <i>Anaphoidea</i> )
<i>compressus</i> (Soyka, 1949: 360) ( <i>Anaphoidea</i> )
<i>crassipilis</i> (Soyka, 1949: 360) ( <i>Anaphoidea</i> )
<i>debilipennis</i> (Soyka, 1949: 361) ( <i>Anaphoidea</i> )
<i>differens</i> (Soyka, 1949: 363) ( <i>Anaphoidea</i> )
<i>exiguus</i> (Soyka, 1949: 363) ( <i>Anaphoidea</i> )
<i>flavitarsis</i> (Soyka, 1949: 364) ( <i>Anaphoidea</i> )
<i>flavicornis</i> (Soyka, 1949: 365) ( <i>Anaphoidea</i> )
<i>globosus</i> (Soyka, 1949: 366) ( <i>Anaphoidea</i> )
<i>kressbachi</i> (Soyka, 1949: 367) ( <i>Anaphoidea</i> )
<i>lineipennis</i> (Soyka, 1949: 368) ( <i>Anaphoidea</i> )
<i>longior</i> (Soyka, 1949: 369) ( <i>Anaphoidea</i> )
<i>longipennis</i> (Soyka, 1949: 370) ( <i>Anaphoidea</i> )
<i>lucidus</i> (Soyka, 1949: 370) ( <i>Anaphoidea</i> )
<i>minimus</i> (Soyka, 1949: 371) ( <i>Anaphoidea</i> )
<i>neoflavus</i> (Soyka, 1949: 372) ( <i>Anaphoidea</i> )
<i>neustadii</i> (Soyka, 1949: 373) ( <i>Anaphoidea</i> )
<i>obscurus</i> (Soyka, 1949: 374) ( <i>Anaphoidea</i> )
<i>palliditarsis</i> (Soyka, 1949: 375) ( <i>Anaphoidea</i> )
<i>parciventris</i> (Soyka, 1949: 376) ( <i>Anaphoidea</i> )
<i>pellucens</i> (Soyka, 1949: 377) ( <i>Anaphoidea</i> )
<i>rectipennis</i> (Soyka, 1949: 378) ( <i>Anaphoidea</i> )
<i>reductus</i> (Soyka, 1949: 379) ( <i>Anaphoidea</i> )
<i>semiflavus</i> (Soyka, 1949: 380) ( <i>Anaphoidea</i> )
<i>semimediuss</i> (Soyka, 1949: 381) ( <i>Anaphoidea</i> )
<i>serbiculus</i> (Soyka, 1949: 381) ( <i>Anaphoidea</i> )
<i>similis</i> (Soyka, 1949: 383) ( <i>Anaphoidea</i> )
<i>variatus</i> (Soyka, 1949: 384) ( <i>Anaphoidea</i> )
<i>valkenburgicus</i> (Soyka, 1949: 385) ( <i>Anaphoidea</i> )
<i>elongatus</i> (Soyka, 1949: 390) ( <i>Hofenederia</i> )
<i>maculicornis</i> (Soyka, 1949: 390) ( <i>Hofenederia</i> )
<i>malchinensis</i> (Soyka, 1949: 392) ( <i>Hofenederia</i> )
<i>pinguicornis</i> (Soyka, 1949: 392) ( <i>Hofenederia</i> )
<i>relictus</i> (Soyka, 1949: 393) ( <i>Hofenederia</i> )
<i>rotundipennis</i> (Soyka, 1949: 394) ( <i>Hofenederia</i> )
<i>tenuis</i> (Soyka, 1949: 395) ( <i>Hofenederia</i> )
<i>cinctus</i> (Soyka, 1949: 397) ( <i>Fulmeikiella</i> )
<i>aterrimus</i> (Soyka, 1949: 399) ( <i>Fulmeikiella</i> )
<i>ater</i> (Soyka), 1949: 400 ( <i>Fulmeikiella</i> )
<i>balteatus</i> (Soyka, 1949: 401) ( <i>Fulmeikiella</i> )
<i>campestris</i> (Soyka, 1949: 401) ( <i>Fulmeikiella</i> )
<i>consimilis</i> (Soyka, 1949: 402) ( <i>Fulmeikiella</i> )
<i>devius</i> (Soyka, 1949: 403) ( <i>Fulmeikiella</i> )
<i>discolor</i> (Soyka, 1949: 404) ( <i>Fulmeikiella</i> )
<i>dubius</i> (Soyka, 1949: 405) ( <i>Fulmeikiella</i> )
<i>latus</i> (Soyka, 1949: 406) ( <i>Fulmeikiella</i> )
<i>linearis</i> (Soyka, 1949: 407) ( <i>Fulmeikiella</i> )

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**TABLE 2.** (Continued)

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<i>longicornis</i> (Soyka, 1949: 407) ( <i>Fulmekiella</i> )
<i>malkwitzi</i> (Soyka, 1949: 408) ( <i>Fulmekiella</i> )
<i>minor</i> (Soyka, 1949: 409) ( <i>Fulmekiella</i> )
<i>nigerrimus</i> (Soyka, 1949: 410) ( <i>Fulmekiella</i> )
<i>niger</i> (Soyka, 1949: 411) ( <i>Fulmekiella</i> )
<i>ornatus</i> (Soyka, 1949: 412) ( <i>Fulmekiella</i> )
<i>ovatus</i> (Soyka, 1949: 413) ( <i>Fulmekiella</i> )
<i>pallidus</i> (Soyka, 1949: 414) ( <i>Fulmekiella</i> )
<i>pallidicornis</i> (Soyka, 1949: 415) ( <i>Fulmekiella</i> )
<i>parallelipennis</i> (Soyka, 1949: 415) ( <i>Fulmekiella</i> )
<i>rufus</i> (Soyka, 1949: 416) ( <i>Fulmekiella</i> )
<i>stubaiensis</i> (Soyka, 1949: 417) ( <i>Fulmekiella</i> )
<i>acutiventris</i> (Soyka, 1949: 419) ( <i>Yungaburra</i> )
<i>confertus</i> (Doutt, 1949: 155) ( <i>Anaphoidea</i> ) <b>USA</b>
<i>gerrisophaga</i> (Doutt, 1949: 156) ( <i>Anaphoidea</i> ) <b>USA</b>
<i>longiclava</i> (Doutt, 1949: 158) ( <i>Anaphoidea</i> ) <b>USA</b>
<i>brunneus</i> (Doutt, 1949: 159) ( <i>Anaphoidea</i> ) <b>USA</b>
<i>wolfsithali</i> (Soyka, 1950: 120) ( <i>Stammeriella</i> )
<i>aestivus</i> (Soyka, 1950: 121) ( <i>Antoniella</i> )
<i>declinatus</i> (Soyka, 1950: 121) ( <i>Antoniella</i> )
<i>discolorsimilis</i> (Soyka, 1950: 122) ( <i>Antoniella</i> )
<i>superadditus</i> (Soyka), 1950: 123 ( <i>Mariella</i> )
<i>timidus</i> (Soyka, 1950: 124) ( <i>Mariella</i> )
<i>aequipennatus</i> (Soyka, 1953a: 37) ( <i>Anaphoidea</i> )
<i>aequus</i> (Soyka, 1953a: 37) ( <i>Anaphoidea</i> )
<i>arcuatus</i> (Soyka, 1953a: 38) ( <i>Anaphoidea</i> )
<i>bicolor</i> (Soyka, 1953a: 38) ( <i>Anaphoidea</i> )
<i>crassus</i> (Soyka, 1953a: 38) ( <i>Anaphoidea</i> )
<i>distinctus</i> (Soyka, 1953a: 38) ( <i>Anaphoidea</i> )
<i>duplicatus</i> (Soyka, 1953b: 53) ( <i>Anaphoidea</i> )
<i>exiguosimilis</i> (Soyka, 1953b: 53) ( <i>Anaphoidea</i> )
<i>falsus</i> (Soyka, 1953b: 53) ( <i>Anaphoidea</i> )
<i>fortipennis</i> (Soyka, 1953b: 53) ( <i>Anaphoidea</i> )
<i>gabitzi</i> (Soyka, 1953b: 54) ( <i>Anaphoidea</i> )
<i>swiedecki</i> (Soyka, 1953b: 54) ( <i>Anaphoidea</i> )
<i>longipilis</i> (Soyka, 1954: 60) ( <i>Anaphoidea</i> )
<i>medioacutus</i> (Soyka, 1954: 60) ( <i>Anaphoidea</i> )
<i>nemorosus</i> (Soyka, 1954: 60) ( <i>Anaphoidea</i> )
<i>neobrevior</i> (Soyka, 1954: 60) ( <i>Anaphoidea</i> )
<i>neodistinctus</i> (Soyka, 1954: 60) ( <i>Anaphoidea</i> )
<i>obsoletus</i> (Soyka, 1954: 61) ( <i>Anaphoidea</i> )
<i>ordinarius</i> (Soyka, 1954: 61) ( <i>Anaphoidea</i> )
<i>piceicornis</i> (Soyka, 1954: 61) ( <i>Anaphoidea</i> )
<i>pilosissimus</i> (Soyka, 1954: 61) ( <i>Anaphoidea</i> )
<i>speciosior</i> (Soyka, 1954: 61) ( <i>Anaphoidea</i> )
<i>stratipennis</i> (Soyka, 1954: 62) ( <i>Anaphoidea</i> )
<i>vulgarisimilis</i> (Soyka, 1954: 62) ( <i>Anaphoidea</i> )
<i>weidenhofi</i> (Soyka, 1954: 62) ( <i>Anaphoidea</i> )
<i>wratislawensis</i> (Soyka, 1954: 62) ( <i>Anaphoidea</i> )
<i>depressus</i> (Soyka, 1954: 63) ( <i>Anaphoidea</i> )
<i>specialis</i> (Soyka, 1955: 462) ( <i>Mymar</i> )
<i>antoniae</i> (Soyka, 1955: 463) ( <i>Mymar</i> )
<i>avalae</i> (Soyka, 1955: 464) ( <i>Mymar</i> )
<i>elegans</i> (Soyka, 1955: 465) ( <i>Mymar</i> )
<i>fennicus</i> (Soyka, 1955: 465) ( <i>Mymar</i> )
<i>gracillimus</i> (Soyka, 1955: 466) ( <i>Mymar</i> )
<i>longispinosus</i> (Soyka, 1955: 467) ( <i>Mymar</i> )

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**TABLE 2.** (Continued)

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<i>luteicornis</i> (Soyka, 1955: 467) ( <i>Mymar</i> )
<i>mirabilis</i> (Soyka, 1955: 468) ( <i>Mymar</i> )
<i>neoserenus</i> (Soyka, 1955: 469) ( <i>Mymar</i> )
<i>neospecialis</i> (Soyka, 1955: 469) ( <i>Mymar</i> )
<i>serenus</i> (Soyka, 1955: 471) ( <i>Mymar</i> )
<i>siegerfeldi</i> (Soyka, 1955: 472) ( <i>Mymar</i> )
<i>speciosus</i> (Soyka, 1955: 472) ( <i>Mymar</i> )
<i>thoraciclus</i> (Soyka, 1955: 473) ( <i>Mymar</i> )
<i>wertaneki</i> (Soyka, 1955: 474) ( <i>Mymar</i> )
<i>chrysomelae</i> (Bakkendorf, 1960: 372) ( <i>Anaphoidea</i> )
<i>alaskae</i> Annecke & Doutt, 1961: 47 ( <i>Anaphes</i> ) <b>USA</b>
* <i>amplipennis</i> Oglöblin, 1962: 49 ( <i>Anaphes [Austranaphes]</i> ) <b>Argentina</b>
* <i>nunezi</i> Oglöblin, 1962: 51 ( <i>Anaphes [Austranaphes]</i> ) <b>Argentina</b>
* <i>pucarobius</i> Oglöblin, 1962: 52 ( <i>Anaphes [Austranaphes]</i> )
* <i>neuquenensis</i> Oglöblin, 1962: 54 ( <i>Anaphes [Austranaphes]</i> ) <b>Argentina</b>
<i>latipterus</i> Bočoc, 1962: 111 ( <i>Anaphes</i> )
<i>heterotomus</i> (Mathot, 1969: 16) ( <i>Patasson</i> )
<i>dessarti</i> (Mathot, 1969: 18) ( <i>Patasson</i> )
<i>tarsalis</i> Mathot, 1969: 19 ( <i>Anaphes</i> )
<i>lemae</i> Bakkendorf, 1970: 153 ( <i>Anaphes</i> )
* <i>tasmaniae</i> Huber & Prinsloo, 1990: 338 ( <i>Anaphes</i> ) <b>Australia</b>
* <i>inexpectatus</i> Huber & Prinsloo, 1990: 340 ( <i>Anaphes</i> ) <b>Australia</b>
<i>byrrhidiphagus</i> Huber, 1992: 43 ( <i>Anaphes</i> ) <b>USA</b>
<i>listronoti</i> Huber in Huber <i>et al.</i> , 1997: 963 ( <i>Anaphes</i> ) <b>Canada</b>
<i>victus</i> Huber in Huber <i>et al.</i> , 1997: 967 ( <i>Anaphes</i> ) <b>Canada</b>
<i>cotei</i> Huber in Huber <i>et al.</i> , 1997: 970 ( <i>Anaphes</i> ) <b>Canada</b>
<i>trijohanni</i> Jesu, 2002: 67 ( <i>Anaphes</i> )
<i>maradonae</i> Jesu, 2003: 107 ( <i>Anaphes</i> )
* <i>fijiensis</i> Huber, 2009: 22 ( <i>Anaphes</i> ) <b>Fiji</b>
<i>germaniacus</i> Özdi̇kmen, 2011: 839 ( <i>Anaphes</i> ) (replacement name for <i>angustipennis</i> Soyka)
<i>soykai</i> Özdi̇kmen, 2011: 839 ( <i>Anaphes</i> ) (replacement name for <i>crassicornis</i> Soyka)
<i>eulongicornis</i> Özdi̇kmen, 2011: 839 ( <i>Anaphes</i> ) (replacement name for <i>longicornis</i> Soyka)
<i>quinquearticulatus</i> Huber & Triapitsyn, 2017: 44 ( <i>Anaphes</i> ) <b>Republic of the Congo</b>

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**TABLE 3.** Available names of nominal species of *Anaphes*, listed first by species in *Anaphes (Anaphes)* followed by species in *Anaphes (Patasson)*. The names in each subgenus are listed in strict chronological order, i.e., by year, by month (if same year), by page (if same publication) and by order of description on page (if same page). Species subsequently placed by Huber (1992) in *Anaphes (Yungaburra)* are identified by an asterisk (\*). The country is given in bold for the 39 non-European species. The two fossil species, *splendens* Meunier, 1901 and *schellwieniens* Meunier, 1901, are not listed here (they are almost certainly not *Anaphes*) but are discussed in Table 6.

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<b><i>Anaphes (Anaphes)</i></b> (85 nominal species/subspecies + 2 replacement names)
<i>fuscipennis</i> Haliday, 1833: 346 ( <i>Anaphes</i> )
<i>flavipes</i> (Foerster, 1841: 43) ( <i>Gonatocerus</i> )
<i>parvus</i> (Foerster, 1841: 43) ( <i>Gonatocerus</i> )
<i>regulus</i> Walker, 1846: 52 ( <i>Anaphes</i> )
<i>auripes</i> Walker, 1846: 52 ( <i>Anaphes</i> )
<i>brevis</i> Walker, 1846: 52 ( <i>Anaphes</i> )
<i>latipennis</i> Walker, 1846: 52 ( <i>Anaphes</i> )
<i>pratensis</i> Foerster, 1847: 211 ( <i>Anaphes</i> )
<i>autumnalis</i> Foerster, 1847: 212 ( <i>Anaphes</i> )
<i>congener</i> Förster, 1861: 42 ( <i>Anaphes</i> )
<i>basalis</i> Förster, 1861: 42 ( <i>Anaphes</i> )
<i>sinipennis</i> Girault, 1911b: 280 ( <i>Anaphes</i> ) <b>USA</b>
<i>nigrellus</i> Girault, 1911b: 282 ( <i>Anaphes</i> ) <b>USA</b>

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**TABLE 3.** (Continued)

- iole* Girault, 1911b: 284 (*Anaphes*) **USA**  
*hercules* Girault, 1911b: 285 (*Anaphes*) **USA**  
*peyerimhoffi* (Kieffer), 1913: 101) (*Clinomymar*) **Algeria**  
*saintpierrei* Girault, 1913: 117 (*Anaphes*) **Australia**  
*ovijentatus* (Crosby & Leonard, 1914: 181) (*Anagrus*) **USA**  
*perdubius* Girault, 1916: 6 (*Anaphes*) **USA**  
*comosipennis* Girault, 1917: 17 (*Anaphes*) **Tanzania**  
*iole anomocerus* Girault, 1929: 13 (*Anaphes*) **USA**  
*behmani* Girault, 1929: 14 (*Anaphes*) **USA**  
*nipponicus* Kuwayama, 1932: 93 (*Anaphes*) **Japan**  
*medius* (Soyka, 1946a: 40) (*Synanaphes*)  
*crassipennis* (Soyka, 1946a: 41) (*Mymar*)  
*ovipositor* (Soyka, 1946a: 41) (*Ferrierella*)  
*ferrierei* (Soyka, 1946b: 180) (*Mymar*)  
*ranalteri* (Soyka, 1946b: 181) (*Synanaphes*)  
*neopratensis* (Soyka, 1946b: 182) (*Ferrierella*)  
*cultripennis* Debauche, 1948: 162 *Anaphes* (*Anaphes*)  
*stygius* Debauche, 1948: 165 *Anaphes* (*Anaphes*)  
*arenbergi* Debauche, 1948: 166 *Anaphes* (*Anaphes*)  
*aries* Debauche, 1948: 168 *Anaphes* (*Anaphes*)  
*gauthieri* Debauche, 1948: 171 *Anaphes* (*Anaphes*)  
*pulcher* (Soyka, 1949: 312) (*Mymar*)  
*acutipennis* (Soyka, 1949: 315) (*Mymar*)  
*brevicornis* (Soyka, 1949: 316) (*Mymar*)  
*ciliatus* (Soyka, 1949: 317) (*Mymar*)  
*crassicornis* (Soyka, 1949: 318) (*Mymar*)  
*ensipennis* (Soyka, 1949: 320) (*Mymar*)  
*flavus* (Soyka, 1949: 321) (*Mymar*)  
*globosicornis* (Soyka, 1949: 322) (*Mymar*)  
*gracilior* (Soyka), 1949: 323 (*Mymar*)  
*leonhardwitzi* (Soyka, 1949: 324) (*Mymar*)  
*nigricornis* (Soyka, 1949: 325) (*Mymar*)  
*pilicornis* (Soyka, 1949: 326) (*Mymar*)  
*piliscapus* (Soyka, 1949: 327) (*Mymar*)  
*pilosipennis* (Soyka, 1949: 328) (*Mymar*)  
*quadraticornis* (Soyka, 1949: 329) (*Mymar*)  
*spinosus* (Soyka, 1949: 330) (*Mymar*)  
*sulphuripes* (Soyka, 1949: 330) (*Mymar*)  
*lacensis* (Soyka, 1949: 335) (*Synanaphes*)  
*angustipennis* (Soyka, 1949: 339) (*Ferrierella*)  
*brevitarsis* (Soyka, 1949: 340) (*Ferrierella*)  
*breviventris* (Soyka, 1949: 341) (*Ferrierella*)  
*capitulatus* (Soyka, 1949: 341) (*Ferrierella*)  
*dilatatus* (Soyka, 1949: 342) (*Ferrierella*)  
*filicornis* (Soyka, 1949: 343) (*Ferrierella*)  
*intermedius* (Soyka, 1949: 344) (*Ferrierella*)  
*laticornis* (Soyka, 1949: 345) (*Ferrierella*)  
*maculatus* (Soyka, 1949: 345) (*Ferrierella*)  
*pulchripennis* (Soyka, 1949: 348) (*Ferrierella*)  
*stammeri* (Soyka, 1949: 349) (*Ferrierella*)  
*tenuipennis* (Soyka, 1949: 350) (*Ferrierella*)  
*varicolor* (Soyka, 1949: 350) (*Ferrierella*)  
*wolfsthali* (Soyka, 1950: 120) (*Stammeriella*)  
*specialis* (Soyka, 1955: 462) (*Mymar*)  
*antoniae* (Soyka, 1955: 463) (*Mymar*)  
*avalae* (Soyka, 1955: 464) (*Mymar*)  
*elegans* (Soyka, 1955: 465) (*Mymar*)

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**TABLE 3.** (Continued)

- fennicus* (Soyka, 1955: 465) (*Mymar*)  
*gracillimus* (Soyka, 1955: 466) (*Mymar*)  
*longispinosus* (Soyka, 1955: 467) (*Mymar*)  
*luteicornis* (Soyka, 1955: 467) (*Mymar*)  
*mirabilis* (Soyka, 1955: 468) (*Mymar*)  
*neoserenus* (Soyka, 1955: 469) (*Mymar*)  
*neospecialis* (Soyka, 1955: 469) (*Mymar*)  
*serenus* (Soyka, 1955: 471) (*Mymar*)  
*siegerfeldi* (Soyka, 1955: 472) (*Mymar*)  
*speciosus* (Soyka, 1955: 472) (*Mymar*)  
*thoracicus* (Soyka, 1955: 473) (*Mymar*)  
*wertaneki* (Soyka, 1955: 474) (*Mymar*)  
*alaskae* Annecke & Doutt, 1961: 47 (*Anaphes*) **USA**  
\**amplipennis* Ogloblin, 1962: 49 *Anaphes (Austranaphes)* **Argentina**  
\**nunezi* Ogloblin, 1962: 51 *Anaphes (Austanaphes)* **Argentina**  
\**pucarobius* Ogloblin, 1962: 52 *Anaphes (Austanaphes)* **Argentina**  
\**neuquenensis* Ogloblin, 1962: 54 *Anaphes (Austranaphes)* **Argentina**  
*sibbei* (Soyka, 1964: 64) (*Anaphoidea*)  
*tarsalis* Mathot, 1969: 19 (*Anaphes*)  
*lemae* Bakkendorf, 1970: 153 (*Anaphes*)  
*byrrhidiphagus* Huber, 1992: 43 (*Anaphes*) **USA**  
\**fijiensis* Huber, 2009: 22 (*Anaphes*) **Fiji**  
*germaniacus* Özdkmen, 2011: 839 (*Anaphes*) (replacement name for *angustipennis* Soyka)  
*soykai* Özdkmen, 2011: 839 (*Anaphes*) (replacement name for *crassicornis* Soyka)  
*quinquearticulatus* Huber & Triapitsyn, 2017: 44 (*Anaphes*) **Republic of the Congo**
- Anaphes (Patasson)** (137 nominal species + 1 replacement name)
- collinus* Walker, 1846: 52 (*Anaphes*)  
*longicornis* Walker, 1846: 52 (*Anaphes*)  
*crassicornis* (Walker, 1846: viii) (*Patasson*), Walker (1846: 52) (*Panthus*)  
*fabarius* (Rondani, 1877: 180) (*Flabrinus*)  
*pallipes* (Ashmead, 1887: 193) (*Alaptus*) **USA**  
*conotracheli* Girault, 1905: 220 (*Anaphes*) **USA**  
*sordidatus* (Girault, 1909: 169) (*Anaphoidea*) **USA**  
*pullicrurus* Girault, 1910: 252 (*Anaphoidea*) **USA**  
*diana* (Girault, 1911a: 215) (*Anaphoidea*)  
\**galtoni* (Girault, 1912: 152) (*Anaphoidea*) **Australia**  
*linnaei* Girault, 1912: 153 (*Anaphoidea*) **Australia**.  
*atomarius* (Brèthes, 1913: 100) (*Anaphoidea*) **Argentina**  
*luna* (Girault, 1914b: 109) (*Anaphoidea*)  
*australia* (Girault, 1920: 97) (*Anaphoidea*) **Australia**  
*calendrae* (Gahan, 1927: 32) (*Anaphoidea*) **USA**  
\**nitens* (Girault, 1928: 262) (*Anaphoidea*) **Australia**  
\**gonipteri* (Ferrière, 1930: 38) (*Anaphoidea*) **Australia**  
*archetti* Ghidini, 1945: 39 (*Anaphes*)  
*silesicus* (Soyka, 1946a: 42) (*Anaphoidea*)  
*vulgaris* (Soyka, 1946a: 42) (*Anaphoidea*)  
*pannonicus* (Soyka), 1946a: 42 (*Anaphoidea*)  
*pectoralis* (Soyka, 1946b: 183) (*Hofenederia*)  
*hundsheimensis* (Soyka, 1946b: 184) (*Fulmekiella*)  
*uryale* Debauche, 1948: 174 *Anaphes (Patasson)*  
*brachygaster* Debauche, 1948: 176 *Anaphes (Patasson)*  
*devillei* Debauche, 1948: 177 *Anaphes (Patasson)*  
*dorcas* Debauche, 1948: 179 *Anaphes (Patasson)*  
*calvescens* Debauche, 1948: 180 *Anaphes (Patasson)*  
*lameerei* Debauche, 1948: 182 *Anaphes (Patasson)*  
*angustipennis* Debauche, 1948: 184 *Anaphes (Patasson)*

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**TABLE 3.** (Continued)

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<i>maialis</i> Debauche, 1948: 185 <i>Anaphes</i> ( <i>Patasson</i> )
<i>leptoceras</i> Debauche, 1948: 187 <i>Anaphes</i> ( <i>Patasson</i> )
<i>additus</i> (Soyka, 1949: 354) ( <i>Anaphoidea</i> )
<i>albipes</i> (Soyka, 1949: 355) ( <i>Anaphoidea</i> )
<i>apilosus</i> (Soyka, 1949: 356) ( <i>Anaphoidea</i> )
<i>brevior</i> (Soyka, 1949: 357) ( <i>Anaphoidea</i> )
<i>communis</i> (Soyka, 1949: 358) ( <i>Anaphoidea</i> )
<i>compressus</i> (Soyka, 1949: 360) ( <i>Anaphoidea</i> )
<i>crassipilis</i> (Soyka, 1949: 360) ( <i>Anaphoidea</i> )
<i>debilipennis</i> (Soyka, 1949: 361) ( <i>Anaphoidea</i> )
<i>differens</i> (Soyka, 1949: 363) ( <i>Anaphoidea</i> )
<i>exiguus</i> (Soyka, 1949: 363) ( <i>Anaphoidea</i> )
<i>flavitarsis</i> (Soyka, 1949: 364) ( <i>Anaphoidea</i> )
<i>flavicornis</i> (Soyka, 1949: 365) ( <i>Anaphoidea</i> )
<i>globosus</i> (Soyka, 1949: 366) ( <i>Anaphoidea</i> )
<i>kressbachii</i> (Soyka, 1949: 367) ( <i>Anaphoidea</i> )
<i>lineipennis</i> (Soyka, 1949: 368) ( <i>Anaphoidea</i> )
<i>longior</i> (Soyka, 1949: 369) ( <i>Anaphoidea</i> )
<i>longipennis</i> (Soyka, 1949: 370) ( <i>Anaphoidea</i> )
<i>lucidus</i> (Soyka, 1949: 370) ( <i>Anaphoidea</i> )
<i>minimus</i> (Soyka, 1949: 371) ( <i>Anaphoidea</i> )
<i>neoflavus</i> (Soyka, 1949: 372) ( <i>Anaphoidea</i> )
<i>neustadtii</i> (Soyka, 1949: 373) ( <i>Anaphoidea</i> )
<i>obscurus</i> (Soyka, 1949: 374) ( <i>Anaphoidea</i> )
<i>palliditarsis</i> (Soyka, 1949: 375) ( <i>Anaphoidea</i> )
<i>parciventris</i> (Soyka, 1949: 376) ( <i>Anaphoidea</i> )
<i>pellucens</i> (Soyka, 1949: 377) ( <i>Anaphoidea</i> )
<i>rectipennis</i> (Soyka, 1949: 378) ( <i>Anaphoidea</i> )
<i>reductus</i> (Soyka, 1949: 379) ( <i>Anaphoidea</i> )
<i>semiflavus</i> (Soyka, 1949: 380) ( <i>Anaphoidea</i> )
<i>semimediuss</i> (Soyka, 1949: 381) ( <i>Anaphoidea</i> )
<i>serbicu</i> s (Soyka, 1949: 381) ( <i>Anaphoidea</i> )
<i>similis</i> (Soyka, 1949: 383) ( <i>Anaphoidea</i> )
<i>variatus</i> (Soyka, 1949: 384) ( <i>Anaphoidea</i> )
<i>valkenburgicus</i> (Soyka, 1949: 385) ( <i>Anaphoidea</i> )
<i>elongatus</i> (Soyka, 1949: 390) ( <i>Hofenederia</i> )
<i>maculicornis</i> (Soyka, 1949: 390) ( <i>Hofenederia</i> )
<i>malchinensis</i> (Soyka, 1949: 392) ( <i>Hofenederia</i> )
<i>pinguicornis</i> (Soyka, 1949: 392) ( <i>Hofenederia</i> )
<i>relictus</i> (Soyka, 1949: 393) ( <i>Hofenederia</i> )
<i>rotundipennis</i> (Soyka, 1949: 394) ( <i>Hofenederia</i> )
<i>tenuis</i> (Soyka, 1949: 395) ( <i>Hofenederia</i> )
<i>cinctus</i> (Soyka, 1949: 397) ( <i>Fulmekiella</i> )
<i>aterrimus</i> (Soyka, 1949: 399) ( <i>Fulmekiella</i> )
<i>ater</i> (Soyka, 1949, 400) ( <i>Fulmekiella</i> )
<i>balteatus</i> (Soyka, 1949: 401) ( <i>Fulmekiella</i> )
<i>campestris</i> (Soyka, 1949: 401) ( <i>Fulmekiella</i> )
<i>consimilis</i> (Soyka, 1949: 402) ( <i>Fulmekiella</i> )
<i>devius</i> (Soyka, 1949: 403) ( <i>Fulmekiella</i> )
<i>discolor</i> (Soyka, 1949: 404) ( <i>Fulmekiella</i> )
<i>dubius</i> (Soyka, 1949: 405) ( <i>Fulmekiella</i> )
<i>latus</i> (Soyka, 1949: 406) ( <i>Fulmekiella</i> )
<i>linearis</i> (Soyka, 1949: 407) ( <i>Fulmekiella</i> )
<i>longicornis</i> (Soyka, 1949: 407) ( <i>Fulmekiella</i> )
<i>malkwitzi</i> (Soyka, 1949: 408) ( <i>Fulmekiella</i> )
<i>minor</i> (Soyka, 1949: 409) ( <i>Fulmekiella</i> )
<i>nigerrimus</i> (Soyka, 1949: 410) ( <i>Fulmekiella</i> )

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**TABLE 3.** (Continued)

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<i>niger</i> (Soyka, 1949: 411) ( <i>Fulmekiella</i> )
<i>ornatus</i> (Soyka), 1949: 412 ( <i>Fulmekiella</i> )
<i>ovatus</i> (Soyka, 1949: 413) ( <i>Fulmekiella</i> )
<i>pallidus</i> (Soyka, 1949: 414) ( <i>Fulmekiella</i> )
<i>pallidicornis</i> (Soyka, 1949: 415) ( <i>Fulmekiella</i> )
<i>parallelipennis</i> (Soyka, 1949: 415) ( <i>Fulmekiella</i> )
<i>rufus</i> (Soyka, 1949: 416) ( <i>Fulmekiella</i> )
<i>stubaiensis</i> (Soyka, 1949: 417) ( <i>Fulmekiella</i> )
<i>acutiventris</i> (Soyka, 1949: 419) ( <i>Yungaburra</i> )
<i>confertus</i> (Doutt, 1949: 155) ( <i>Anaphoidea</i> ) <b>USA</b>
<i>gerrisophaga</i> (Doutt, 1949: 156) ( <i>Anaphoidea</i> ) <b>USA</b>
<i>longiclava</i> (Doutt, 1949: 158) ( <i>Anaphoidea</i> ) <b>USA</b>
<i>brunneus</i> (Doutt, 1949: 159) ( <i>Anaphoidea</i> ) <b>USA</b>
<i>aestivus</i> (Soyka, 1950: 121) ( <i>Antoniella</i> )
<i>declinatus</i> (Soyka, 1950: 121) ( <i>Antoniella</i> )
<i>discolorsimilis</i> (Soyka, 1950: 122) ( <i>Antoniella</i> )
<i>superadditus</i> (Soyka, 1950: 123) ( <i>Mariella</i> )
<i>timidus</i> (Soyka, 1950: 124) ( <i>Mariella</i> )
<i>aequipennatus</i> (Soyka, 1953a: 37) ( <i>Anaphoidea</i> )
<i>aequus</i> (Soyka, 1953a: 37) ( <i>Anaphoidea</i> )
<i>arcuatus</i> (Soyka, 1953a: 38) ( <i>Anaphoidea</i> )
<i>bicolor</i> (Soyka, 1953a: 38) ( <i>Anaphoidea</i> )
<i>crassus</i> (Soyka, 1953a: 38) ( <i>Anaphoidea</i> )
<i>distinctus</i> (Soyka, 1953a: 38) ( <i>Anaphoidea</i> )
<i>duplicatus</i> (Soyka, 1953b: 53) ( <i>Anaphoidea</i> )
<i>exiguosimilis</i> (Soyka, 1953b: 53) ( <i>Anaphoidea</i> )
<i>falsus</i> (Soyka, 1953b: 53) ( <i>Anaphoidea</i> )
<i>fortipennis</i> (Soyka, 1953b: 53) ( <i>Anaphoidea</i> )
<i>gabitzi</i> (Soyka, 1953b: 54) ( <i>Anaphoidea</i> )
<i>swiedecki</i> (Soyka, 1953b: 54) ( <i>Anaphoidea</i> )
<i>longipilis</i> (Soyka, 1954: 60) ( <i>Anaphoidea</i> )
<i>medioacutus</i> (Soyka, 1954: 60) ( <i>Anaphoidea</i> )
<i>nemorosus</i> (Soyka, 1954: 60) ( <i>Anaphoidea</i> )
<i>neobrevior</i> (Soyka, 1954: 60) ( <i>Anaphoidea</i> )
<i>neodistinctus</i> (Soyka, 1954: 60) ( <i>Anaphoidea</i> )
<i>obsoletus</i> (Soyka, 1954: 61) ( <i>Anaphoidea</i> )
<i>ordinarius</i> (Soyka, 1954: 61) ( <i>Anaphoidea</i> )
<i>piceicornis</i> (Soyka, 1954: 61) ( <i>Anaphoidea</i> )
<i>pilosissimus</i> (Soyka, 1954: 61) ( <i>Anaphoidea</i> )
<i>speciosior</i> (Soyka, 1954: 61) ( <i>Anaphoidea</i> )
<i>stratipennis</i> (Soyka, 1954: 62) ( <i>Anaphoidea</i> )
<i>vulgarisimilis</i> (Soyka, 1954: 62) ( <i>Anaphoidea</i> )
<i>weidenhofi</i> (Soyka, 1954: 62) ( <i>Anaphoidea</i> )
<i>wratislawensis</i> (Soyka, 1954: 62) ( <i>Anaphoidea</i> )
<i>depressus</i> (Soyka, 1954: 63) ( <i>Anaphoidea</i> )
<i>chrysomelae</i> (Bakkendorf, 1960: 372) ( <i>Anaphoidea</i> )
<i>latipterus</i> Bočec, 1962: 111 ( <i>Anaphes</i> )
<i>heterotomus</i> (Mathot, 1969: 16) ( <i>Patasson</i> )
<i>dessarti</i> (Mathot, 1969: 18) ( <i>Patasson</i> )
* <i>tasmaniae</i> Huber & Prinsloo, 1990: 338 ( <i>Anaphes</i> ) <b>Australia</b>
* <i>inexpectatus</i> Huber & Prinsloo, 1990: 340 ( <i>Anaphes</i> ) <b>Australia</b>
<i>listronoti</i> Huber, 1997: 963 ( <i>Anaphes</i> ) <b>Canada</b>
<i>victus</i> Huber, 1997: 967 ( <i>Anaphes</i> ) <b>Canada</b>
<i>cotei</i> Huber, 1997: 970 ( <i>Anaphes</i> ) <b>Canada</b>
<i>trijohanni</i> Jesu, 2002: 67 ( <i>Anaphes</i> )
<i>maradonae</i> Jesu, 2003: 107 ( <i>Anaphes</i> )
<i>eulongicornis</i> Özdikmen, 2011: 839 ( <i>Anaphes</i> ) (replacement name for <i>longicornis</i> Soyka)

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**TABLE 4.** Primary type localities for 231 nominal species/subspecies of world *Anaphes*, listed alphabetically after each locality. Latitudes and longitudes are taken from Google Earth and rounded to the nearest minute. Australian localities and their coordinates are taken from Dahms (1978). Localities for *auripes*, *basalis*, *congener*, *crassicornis* Walker, *fuscipecten*, *longicornis* Walker, *regulus* and *diana* are uncertain but the likely localities are given. A country only was given for *comosipennis* and *iole anomocerus*. Type localities (not even the country) are unknown for 4 *nomina dubia*: *cinctus*, *depressus*, *pulcher*, and *specialis*. Current locality names or spellings are given in brackets if different from those in descriptions. In particular, the six localities listed for Poland are in Silesia, once part of Germany; the German names for these localities are followed by, in brackets, the corresponding Polish name. One locality that used to be in Serbia is now in Montenegro. The two fossil species, *splendens* Meunier, 1901 and *schellwieniens* Meunier, 1901, are not included (they are almost certainly not *Anaphes*) but are discussed in Table 6.

Published type localities for the 151 nominal species described by Soyka:

- Austria**, Neustift 47°06'N 11°18'E and Krössbach, 47°05'N 11°16'E (these two localities are about 4 km apart in the alpine valley of Stubaital, Tirol): *acutiventris*, *crassus*, *falsus*, *ferrierei*, *flavitarsis*, *kressbachi*, *maculicornis*, *neoflavus*, *neoserenus*, *piceicornis*, *ranalteri*, *rufus*, *speciosus*, *stubaiensis*, *thoracicus*, *timidus*.
- Austria**, Gumpoldskirchen 48°03'N 16°17'E: *swiedecki*.
- Austria**, Hundsheim: 48°07'N 16°56'E: *additus*, *albipes*, *ater*, *aterrimus*, *balteatus*, *bicolor*, *campestris*, *consimilis*, *differens*, *discolor*, *dubius*, *duplicatus*, *elongatus*, *hundsheimensis*, *longispinosus*, *medius*, *minor*, *neodistinctus*, *neopratensis*, *niger*, *nigricornis*, *nigerrimus*, *obscurus*, *ornatus*, *pallidicornis*, *palliditarsis*, *pannonicus*, *pectoralis*, *pinguicornis*, *relictus*, *speciosior*, *spinosus*, *stratipennis*, *tenuis*, *varicolor*.
- Austria**, Jois am Neusiedlersee 47°58'N 16°48'E: *lacensis*, *rotundipennis*.
- Austria**, Siegerfeld 48°02'N 16°10'E: *siegerfeldi*.
- Austria**, Vienna, Leopoldsberg 48°17'N 16°21'E: *pilosipennis*.
- Austria**, Wolfsthal, 48°08'N 17°00'E [Rehfeld, 48°33'N 15°52'E]: *wolfsthalii*.
- Finland**, Luirojärvi [sic] [Luirojärvi (Luiro Lake)], 68°12'N 28°02'E: *acutipennis* [69°10'N 20°E on type slide], *fennicus*.
- Finland**, Mosku at Luirojoki (Luiro River), 67°42'N [68° on type slide] 27°50'E: *crassipennis*.
- Germany**, Erlangen, 49°35'N 11°00'E: *angustipennis* Soyka.
- Germany**, Malchin, Jettchenshof or variants of this on type slides and original descriptions, 53°46'N 12°46'E: *brevitarsis*, *compressus*, *discolorsimilis*, *exiguus*, *flavus*, *gracillimus*, *intermedius*, *malchinensis*, *neospecialis*, *ovipositor*, *parallelipennis*, *pilicornis*, *quadraticornis*, *serenus*, *sulphuripes*, *recipennis*, *variatus*, *wertaneki*.
- Netherlands**, Valkenburg, 50°52'N 5°50'E: *aequipennatus*, *antoniae*, *apilosus*, *arcuatus*, *brevior*, *brevicornis*, *breviventris*, *capitulatus*, *communis*, *debilipennis*, *declinatus*, *dilatatus*, *devius*, *distinctus*, *elegans*, *ensipennis*, *filicornis*, *flavicornis*, *fortipennis*, *gracilior*, *laticornis*, *lineipennis*, *longior*, *lucidus*, *luteicornis*, *maculatus*, *medioacutus*, *minimus*, *obsoletus*, *ordinarius*, *pallidus*, *parciventris*, *pellucens*, *piliscapus*, *reductus*, *semiflavus*, *semimediatus*, *similis*, *tenuihornis*, *valkenburgicus*, *vulgaris*, *vulgarisimilis*.
- Poland**, Breslau [Wrocław], 51°06'N 17°01'E, (including Grüneiche, Leonhardwitz, Wiedenhof): *aestivus*, *ciliatus*, *crassipilis*, *gabizzi*, *leonhardwitzi*, *longipilis*, *nemorosus*, *pulchripennis*, *silesicus*, *stammeri*, *weidenhofi*, *wratislawensis*.
- Poland**, Bruschewitz [Pruszowice], 51°11'N 17°08'E: *crassicornis* Soyka.
- Poland**, Malkwitz [Malkowice], 51°05'N 16°49'E: *aequus*, *exiguosimilis*, *globosus*, *latus*, *longicornis* Soyka, *malkwitzi*, *ovatus*, *superadditus*.
- Poland**, Neustadt [Prudnik], 50°19'N 17°34'W: *linearis*, *longipennis*, *neobrevior*, *neustadtii*, *pilosissimus*.
- Poland**, Ramischau [Ramiszów], 51°12'N 17°05'E: *mirabilis*.
- Poland**, Schlawasee [Sława Lake, Jezioro Sławskie], 51°52'N 16°04'E: *globosicornis*.
- Serbia**, Andrejanica [**Montenegro**, Andrijevica], 42°44'N 19°47'30"E: *serbicu*.
- Serbia**, Belgrade, Avala Berg [Put za Avalu (Mt. Avala)], 44°41'N 20°31'E: *avalae*.

Type localities for the 80 nominal species (including 1 subspecies) described by authors other than Soyka:

- Algeria**, Azerou Tidjer, near Tirourda Pass, 36°38'N 4°21'E: *peyerimhoffi*.
- Argentina**, Buenos Aires, General Urquiza, 34°34'S 58°29'W: *atomarius*.
- Argentina**, Neuquén, Pucará, Lago Lácar, 40°09'S 71°30'W: *amplipennis*, *neuquenensis*, *pucarobius*.
- Argentina**, Tierra del Fuego, Bahía, Aguirre, 54°49'S 68°20'W: *nunezi*.
- Australia**, Queensland, Gordonvale, 17°05'S 145°47'E (Dahms 1978): *australia*, *linnaei*.
- Australia**, Queensland, Harvey's Creek, 17°16'S 145°55'E (Dahms 1978): *saintpierrei*.
- Australia**, Queensland, Roma, 26°35'S 148°47'E (Dahms 1978): *galtoni*.
- Australia**, Tasmania, Black Charles Opening, 42°40'S 147°31'E: *tasmaniae*.
- Australia**, Tasmania, Hobart, 42°52'S 147°18'E and Fingal, 41°38'S 147°58'E: *inexpectatus*.

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**TABLE 4.** (Continued)

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<b>Australia</b> , Victoria, Fern Tree Gully, 37°53'S 145°18'E: <i>gonipteri, nitens</i> .
<b>Belgium</b> , Egenhoven, 50°52'N 4°39'E: <i>aries, maialis</i> .
<b>Belgium</b> , Heverlee, 50°52'N 4°41'E: <i>brachygaster, calvescens, cultripennis, dorcus, gauthieri, lameerei, leptoceras</i> .
<b>Belgium</b> , Hour, 50°10'N 5°02'E: <i>dessarti, heterotomus</i> .
<b>Belgium</b> , Kessel-Lo, 50°53'N 4°44'E: <i>angustipennis</i> Debauche, <i>stygius</i> .
<b>Belgium</b> , Loverval Forest, 50°22'N 4°28'E: <i>devillei, euryale</i> .
<b>Belgium</b> , Meerdael Forest, 50°49'N 4°42'E: <i>arenbergi</i> .
<b>Canada</b> ' Nova Scotia, Great Village, 45°25'N 63°36'W: <i>cotei</i> .
<b>Canada</b> , Quebec, Ste. Clotilde, 45°10'N 73°40'W: <i>listronoti, victus</i> .
<b>England (UK)</b> , Middlesex, Southgate vicinity: 51°33'N 0°11'E (Graham 1982: 192): <i>auripes, crassicornis</i> Walker, <i>fuscipennis, longicornis</i> Walker, <i>regulus</i> .
<b>England (UK)</b> , Woking 51°19'N 00°34'E or Holloway, 51°33'N 00°07'E (Enock 1909: 450): <i>diana</i> .
<b>Fiji</b> , Vanua Levu, Bua, Kilaka, 16°48'S 178°59'E: <i>fijiensis</i> .
<b>France</b> , Fontainbleau Forest: 48°23'N 2°37'E: <i>brevis, latipennis</i> .
<b>Germany</b> , Aachen and vicinity, 50°46'N 6°05'E: <i>autumnalis, flavipes, parvus, pratensis</i> .
<b>Northern Ireland (UK)</b> , Belfast, Cavehill: 54°39'30"N 5°57'E: <i>collinus</i> .
<b>Italy</b> , Agro Pontino, Littoria [Latina], 41°23'N 13°03'E: <i>archettii</i> .
<b>Italy</b> , Bocca di Magra, 44°03'N 9°58'E: <i>chrysomelae</i> .
<b>Italy</b> , Parma and vicinity, 44°48'N 10°20'E (Bouček 1974): <i>fabarius</i> .
<b>Italy</b> , Portici, 40°49'N 14°20'E (Webster 1912): <i>luna, trijohanni</i> .
<b>Italy</b> , Sibari, 39°45'N 16°29'E: <i>maradonae</i> .
<b>Japan</b> , Ôno, Kameda District, 41°56'N 149°41'E and Kagura, Kamikawa District, 43°46'N 142°144'E: <i>nipponicus</i> .
<b>Norway</b> , Vassbyda [Vassbygdi] (Flám), 60°52'N 7°07'E [Vassbygda, 63°37'N 9°38'E, description of type locality ambiguous; the former is most likely]: <i>tarsalis</i> .
<b>Poland</b> , Lublin, 51°15'N 22°34'E: <i>lemae</i> .
<b>Republic of the Congo</b> , Lesio-Louna Park, 3°6'1"S 15°31'26"E: <i>quinquearticulatus</i> .
<b>Romania</b> , Cluj [Cluj-Napoka], Someş [River], 46°46'N 23°32'E: <i>latipterus</i> .
<b>Switzerland</b> , likely the Canton of Graubunden, possibly Rosegthal (Roseg Valley)near Pontresina, 46°27'N 9°52'E: <i>basalis, congener</i> .
<b>Tanzania</b> , no locality specified: <i>comosipennis</i> .
<b>USA</b> , Alaska, Point Barrow, 71°23'N 156°29'W: <i>alaskae</i> .
<b>USA</b> , California, Forrestville, 38°28'N 122°53'W: <i>brunneus</i> .
<b>USA</b> , California, Lake Britton, 41°02'N 121°39'W: <i>gerrisophaga</i> .
<b>USA</b> , California, Morgan Hill, 37°08'N 121°39'W: <i>longiclava</i> .
<b>USA</b> , California, Oakville, 38°26'N 122°24'W: <i>confertus</i> .
<b>USA</b> , Florida, Jacksonville, 31°20'N 81°39'W: <i>pallipes</i> .
<b>USA</b> , Illinois, Centralia, 38°32'N 89°08'W: <i>pullicrurus, sordidatus</i> .
<b>USA</b> , Illinois, Urbana, 40°06'N 88°14'W: <i>hercules, iole, nigrellus, sinipennis</i> .
<b>USA</b> , Maryland, Arundel, 38°57'N 76°33'W: <i>conotrachelii</i> .
<b>USA</b> , Missouri, Kirkwood, 38°35'N 90°24'W: <i>calendrae</i> .
<b>USA</b> , New York, Ithaca, 42°27'N 76°30'W: <i>behmani, ovijentatus</i> .
<b>USA</b> , Oregon, Mary's Peak, 44°30'N 123°33'W: <i>byrrhidiphagus</i> .
<b>USA</b> , Utah, Salt Lake City, 40°46'N 111°53'W: <i>perdubius</i> .
<b>USA</b> , no locality specified: <i>iole anomocerus</i> .

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**TABLE 5.** Primary type localities for nominal species/subspecies of world *Anaphes*, listed chronologically within each subgenus. For the Soyka species, the numbers in parentheses are last two digits of the year of publication and page of the original description, followed by his subsequent description (if any) in brackets. For all the species, the names are listed first for *A. (Anaphes)* species then, separated by a forward slash (/), for *A. (Patasson)* species. If only one species was described from a particular locality or if all the species belong in only one of the subgenera then the forward slash followed by an en dash (/-) is placed after the species if it is (or they are) in *A. (Anaphes)* and an en dash followed by a forward slash (-/) is placed in front of the species if it is (or they are) in *A. (Patasson)*. The two fossil species, *splendens* Meunier, 1901 and *schellwieniens* Meunier, 1901, are not listed here (they are almost certainly not *Anaphes*) but are discussed in Table 6.

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Published type localities for the 151 nominal species described by Soyka:

**Austria**, Gumpoldskirchen 48°03'N 16°17'E: *-/ swiedecki* (53b-54).

**Austria**, Hundsheim: 48°07'N 16°56'E: *medius* (46a-30) [49-334], *neopratensis* (46b-182) [49-338], *nigricornis* (49-325), *spinosus* (49-330), *varicolor* (49-350), *longispinosus* (55-467) / *pannonicus* (46a-42), *pectoralis* (46b-183), *hundsheimensis* (46b-184) [49-398], *additus* (49-354), *albipes* (49-355), *differens* (49-363), *obscurus* (49-374), *palliditarsis* (49-375), *elongatus* (49-390), *pinguicornis* (49-392), *relictus* (49-393), *tenuis* (49-395), *aterrimus* (49-399), *ater* (49-400), *campestris* (49-401), *balteatus* (49-401), *consimilis* (49-402), *discolor* (49-404), *dubius* (49-405), *minor* (49-409), *nigerrimus* (49-410), *niger* (49-411), *ornatus* (49-412), *pallidicornis* (49-415), *bicolor* (53a-38), *duplicatus* (53b-53), *neodistinctus* (54-60), *speciosior* (54-61), *stratipennis* (54-62).

**Austria**, Jois am Neusiedlersee 47°58'N 16°48'E: *lacensis* (49-335) / *rotundipennis* (49-394).

**Austria**, Neustift 47°06'N 11°18'E and Krössbach, 47°05'N 11°16'E. These two localities are about 4 km apart in the alpine valley of Stubaital, Tirol: *ferrierei* (46b-180) [49-313], *ranalteri* (46b-181) (49-333), *neoserenus* (55-469), *speciosus* (55-472), *thoracicus* (55-473) / *flavitaris* (49-364), *kressbachi* (49-367), *neoflavus* (49-372), *maculicornis* (49-390), *rufus* (49-416), *stubaiensis* (49-417), *acutiventris* (49-419), *timidus* (50a-124), *crassus* (53a-38), *falsus* (53b-53), *piceicornis* (54-61).

**Austria**, Siegerfeld 48°02'N 16°10'E: *siegerfeldi* (55-472) /-.

**Austria**, Vienna, Leopoldsberg 48°17'N 16°21'E: *-/ pilosipennis* (49-328).

**Austria**, Wolfsthal, 48°08'N 17°00'E [Rehfeld, 48°33'N 15°52'E]: *wolfsthalii* (50a-120) /-.

**Finland**, Luirojärni (*sic*) [Luirojärvi (Luiro Lake)], 68°12'N 28°02'E: *acutipennis* (49-315), *fennicus* (55-465) /-.

**Finland**, Mosku at Luirojoki (Luiro River), 67°42'N [68° on type slide] 27°50'E: *crassipennis* (46a-41) /-.

**Germany**, Erlangen, 49°35'N 11°00'E: *angustipennis* Soyka (49-339) /-.

**Germany**, Malchin, Jettchenhof, 53°46'N 12°46'E: *ovipositor* (46a-41), *flavus* (49-321), *pilicornis* (49-326), *quadraticornis* (49-329), *sulphuripes* (49-330), *brevitarsis* (49-340), *intermedius* (49-344), *gracillimus* (55-466), *neospecialis* (55-469), *serenus* (55-471), *wertaneki* (55-474) / *compressus* (49-360), *exiguus* (49-363), *rectipennis* (49-378), *variatus* (49-384), *malchinensis* (49-392), *parallelipennis* (49-415), *discolorsimilis* (50a-122).

**Netherlands**, Valkenburg, 50°52'N 5°50'E: *brevicornis* (49-316), *ensipennis* (49-320), *gracilior* (49-323), *piliscapus* (49-327), *breviventris* (49-341), *capitulatus* (49-341), *dilatatus* (49-342), *filicornis* (49-343), *laticornis* (49-345), *maculatus* (49-345), *tenuipennis* (49-350), *antoniae* (55-463), *elegans* (55-465), *luteicornis* (55-467) / *vulgaris* (46a: 42), *apilosus* (49-356), *brevior* (49-357), *communis* (49-358), *debilipennis* (49-361), *flavicornis* (49-365), *lineipennis* (49-368), *longior* (49-369), *lucidus* (49-370), *minimus* (49-371), *parciventris* (49-376), *pellucens* (49-377), *reductus* (49-379), *semiflavus* (49-380), *semimediatus* (49-381), *similis* (49-383), *valkenburgicus* (49-385), *devius* (49-403), *pallidus* (49-414), *declinatus* (50a-121), *aequipennatus* (53a-37), *arcuatus* (53a: 38), *distinctus* (53a-38), *fortipennis* (53b 53), *medioacutus* (54-60), *obsoletus* (54-61), *ordinarius* (54-61), *vulgarisimilis* (54-62).

**Poland**, Breslau [Wrocław], 51°06'N 17°01'E, (including Grüneiche, Leonhardwitz, Wiedenhof): *ciliatus* (49-317), *leonhardwitzii* (49-324), *pulchripennis* (49-348), *stammeri* (49-349) / *silesicus* (46a-42), *crassipilis* (49-360), *aestivus* (50a-121), *gabitzi* (53b-54), *longipilis* (54-60), *nemorosus* (54-60), *weidenhofii* (54-62), *wratislawensis* (54-62).

**Poland**, Bruschewitz [Pruszowice], 51°11'N 17°08'E: *-/ crassicornis* Soyka (49-318).

**Poland**, Malkwitz [Malkowice], 51°05'N 16°49'E: *-/ globosus* (49-366), *latus* (49-406), *longicornis* Soyka (49-407), *malkwitzii* (49-408), *ovatus* (49-413), *superadditus* (50-123), *aequus* (53a-37), *exiguosimilis* (53b-53).

**Poland**, Neustadt [Prudnik], 50°19'N 17°34'W: *-/ longipennis* (49-370), *neustadii* (49-373), *linearis* (49-407), *neobrevior* (54-60), *pilosissimus* (54-61).

**Poland**, Ramischau [Ramiszów], 51°12'N 17°05'E: *mirabilis* (55-468) /-.

**Poland**, Schlawasee [Sława Lake (Jezioro Sławskie)], 51°52'N 16°04'E: *globosicornis* (49-322) /-.

**Serbia**, Andrejanica [Montenegro, Andrijevica], 42°44'N 19°47'30"E: *-/ serbicus* (49-381).

**Serbia**, Belgrade, Avala Berg [Put za Avalu], 44°41'N 20°31'E: *avalae* (55-464) /-.

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**TABLE 5.** (Continued)

Type localities for the 79 nominal species (including 1 subspecies) of *Anaphes* described by authors other than Soyka:

- Algeria**, Azerou Tidjer, near Tirourda Pass, 36°38'N 4°21'E: *peyerimhoffi* /–.
- Argentina**, Buenos Aires, General Urquiza, 34°34'S 58°29'W: –/ *atomarius*.
- Argentina**, Neuquén, Pucará, Lago Lácar, 40°09'S 71°30'W: *amplipennis*, *neuquensis*, *pucarobius* /–.
- Argentina**, Tierra del Fuego, Bahía, Aguirre, 54°49'S 68°20'W: *nunezi* /–.
- Australia**, Queensland, Cairns, Harvey's Creek, 17°16'S 145°55'E (Dahms 1978): *saintpierrei* /–.
- Australia**, Queensland, Gordonvale, 17°05'S 145°47'E (Dahms 1978): –/ *australia*, *linnaei*.
- Australia**, Queensland, Roma, 26°35'S 148°47'E (Dahms 1978): –/ *galtoni*.
- Australia**, Tasmania, Black Charles Opening, 42°40'S 147°31'E: –/ *tasmaniae*.
- Australia**, Tasmania, Hobart, 42°52'S 147°18'E and Fingal, 41°38'S 147°58'E: –/ *inexpectatus*.
- Australia**, Victoria, Fern Tree Gully, 37°53'S 145°18'E: –/ *gonipteri*, *nitens*.
- Belgium**, Egenhoven, 50°52'N 4°39'E: *aries* / *maialis*.
- Belgium**, Heverlee, 50°52'N 4°41'E: *cultripennis*, *gauthieri* / *brachygaster*, *calvescens*, *dorcas*, *lameerei*, *leptoceras*.
- Belgium**, Hour, 50°10'N 5°02'E: –/ *dessarti*, *heterotomus*.
- Belgium**, Kessel-Lo, 50°53'N 4°44'E: *stygius* / *angustipennis* Debauche.
- Belgium**, Loverval Forest, 50°22'N 4°28'E: –/ *devillei*, *curyale*.
- Belgium**, Meerdael Forest, 50°49'N 4°42'E: *arenbergi* /–.
- Canada**, Nova Scotia, Great Village, 45°25'N 63°36'W: –/ *cotei*.
- Canada**, Quebec, Ste. Clotilde, 45°10'N 73°40'W: –/ *listronoti*, *victus*.
- England (UK)**, Middlesex, Southgate vicinity: 51°33'N 0°11'E (Graham 1982: 192): *fuscipennis*, *regulus*, *auripes* / *crassicornis* Walker, *longicornis* Walker.
- England (UK)**, Woking 51°19'N 00°34'E or Holloway, 51°33'N 00°07'E (Enock 1909: 450): –/ *diana*.
- Fiji**, Vanua Levu, Bua, Kilaka, 16°48'S 178°59'E: *fijiensis* /–.
- France**, Fontainbleau Forest: 48°23'N 2°37'E: –/ *brevis*, *latipennis*.
- Germany**, Aachen and vicinity, 50°46'N 6°05'E: *flavipes*, *pratensis*, *autumnalis* / *parvus*.
- Italy**, Agro Pontino, Littoria [Latina], 41°23'N 13°03'E: –/ *archettii*.
- Italy**, Bocca di Magra, 44°03'N 9°58'E: –/ *chrysomelae*.
- Italy**, Parma and vicinity, 44°48'N 10°20'E (Bouček 1974): –/ *fabarius*.
- Italy**, Portici, 40°49'N 14°20'E (Webster 1912): –/ *luna*, *trijohanni*.
- Italy**, Portici, 39°45'N 16°27'E: –/ *maradonae*.
- Japan**, Ōno, Kameda District, 41°56'N 149°41'E and Kagura, Kamikawa District, 43°46'N 142°144'E: *nipponicus* /–.
- Northern Ireland (UK)**, Belfast, Cavehill: 54°39'30"N 5°57'E: –/ *collinus*.
- Norway**, Vassbyda [Vassbygdi] (Flám), 60°52'N 7°07'E [Vassbygda, 63°37'N 9°38'E, description of type locality ambiguous; the former is most likely]: *tarsalis* /–.
- Poland**, Lublin, 51°15'N 22°34'E: *lemae* /–.
- Republic of the Congo**, Lesio-Louna Park, 3°6'1"S 15°31'26"E: *quinquearticulatus* /–.
- Romania**, Cluj [Cluj-Napoca], Someş [River], 46°46'N 23°32'E: –/ *latipterus*.
- Switzerland**, likely Canton of Graubünden, possibly Rosegthal (Roseg Valley) near Pontresina, 46°27'N 9°52'E: *congener*, *basalis* /–.
- Tanzania**, no locality specified: *comosipennis* /–.
- USA**, Alaska, Point Barrow, 71°23'N 156°29'W: *alaskae* /–.
- USA**, California, Forrestville, 38°28'N 122°53'W: –/ *brunneus*.
- USA**, California, Lake Britton, 41°02'N 121°39'W: –/ *gerrisophaga*.
- USA**, California, Morgan Hill, 37°08'N 121°39'W: –/ *longiclava*.
- USA**, California, Oakville, 38°26'N 122°24'W: –/ *confertus*.
- USA**, Florida, Jacksonville, 31°20'N 81°39'W: –/ *pallipes*.
- USA**, Illinois, Centralia, 38°32'N 89°08'W: –/ *pullicrurus*, *sordidatus*.
- USA**, Illinois, Urbana, 40°06'N 88°14'W: *sinipennis*, *nigrellus*, *iole*, *hercules* /–.
- USA**, Maryland, Arundel, 38°57'N 76°33'W: –/ *conotrachelii*.
- USA**, Missouri, Kirkwood, 38°35'N 90°24'W: –/ *calendrae*.
- USA**, New York, Ithaca, 42°27'N 76°30'W: *ovijentatus*, *behmani* /–.
- USA**, Oregon, Mary's Peak, 44°30'N 123°33'W: *byrrhidiphagus* /–.
- USA**, Utah, Salt Lake City, 40°46'N 111°53'W: *perdubius* /–.
- USA**, no locality specified: *iole anomocerus* /–.

**TABLE 6.** Valid *Anaphes* species (in bold) arranged alphabetically, first by those classified in *A. (Anaphes)* second by those classified in *A. (Patasson)*. The species are grouped according to their biogeographical region. Synonyms are listed in strict chronological priority after the valid name. Acronyms (in parentheses) of primary type depository are given after the sex of the primary type(s), followed by [in brackets] the number and sex of secondary types (paratypes, paralectotypes) and type locality, etc., of the primary type(s). For Soyka and Debauche species, if collection information on the type slide differs from the published information or has additional information not stated in the description this is given in brackets, except for “Ignatiuskolleg” (see below). Usually it is only some part of the collection date that differs. Soyka specimens sometimes have the habitat on the holotype slide but not in the description; “ex hay” [out of or ex hay] is treated as a habitat, even if the specimens were collected on a window. Soyka’s specimens from Valkenburg almost all came from a window or windows of “Ignatiuskolleg”; this was not stated under the relevant species descriptions but was often written on the holotype slide, once simply as “Kolleg”. In contrast, the Debauche species have the habitat in the description but not on the holotype slide, i.e., the published information is more complete.

#### *ANAPHES (ANAPHES)*

##### **Afrotropical Region**

*quinqearticulatus* Huber & Triapitsyn, 2017: 44 (*Anaphes*), holotype ♀ (UCRC). **TL:** Republic of the Congo, Pool, Lesio-Louna Park, Abio, 29.vii.2008.

##### **Australian Region**

*fijiensis* Huber, 2009: 22 (*Anaphes*), holotype ♀ (BPBM) [2♀ and 2♂ paratypes]. **TL:** Fiji, Vanua Levu, Dua, Kilaka, 28.vi-2.vii.2004.

*saintpierrei* Girault, 1913: 117 (*Anaphes*), holotype ♀ (QM). **TL:** Australia, Queensland, Harvey’s Creek (Cairns), 13.vii.1913, on hotel window.

##### **Nearctic Region**

*alaskae* Annecke & Doutt, 1961: 47 (*Anaphes*), holotype ♀ (EMEC) [2♂ paratypes]. **TL:** USA, Alaska, Point Barrow, 17.vii.1952.

*behmani* Girault 1929: 246 (*Anaphes*), lectotype ♀ (USNM), designated by Huber 1992: 50 [4♀ and 3♂ paralectotypes]. **TL:** USA, New York, Ithaca, 12.vii, no year, ex larva [!?] of *Dibolia borealis* Chevrolat (Chrysomelidae). Described in key only; locality data and host obtained from type slide.

*byrrhidiphagus* Huber, 1992: 43 (*Anaphes*), holotype ♀ (USNM) [88♀ and 20♂ paratypes]. **TL:** USA, Oregon, Benton Co., Mary’s Peak, 27.iii.1977, ex *Lioligus nitidus* (Motschulsky) (Byrrhidae) in moss.

*hercules* Girault 1911b: 285 (*Anaphes*), holotype ♀ (INHS). **TL:** USA, Illinois, Urbana, on glass side of a greenhouse, 8.vi.1910.

*iole* Girault 1911b: 284 (*Anaphes*), holotype ♀ (INHS), lost. **TL:** USA, Illinois, Urbana, on greenhouse window, 30.iv.1910.

*iole anomocerus* Girault 1929: 13 (*Anaphes*) lectotype ♀ (USNM), designated by Huber, 1992: 42. **TL:** USA, locality not given. Synonymy by Huber & Rajakulendran, 1988: 893.

*oviventatus* (Crosby & Leonard), 1914: 181 (*Anagrus*), lectotype ♀ (CUIC), designated by Huber 1992: 42 [3♀ paralectotypes]. **TL:** USA, New York, Ithaca, 7.x.1913. Synonymy by Girault, 1929: 14.

*perdubius* Girault 1916: 6 (*Anaphes*), holotype ♀ (USNM). **TL:** USA, Utah, Salt Lake City, 2.ix.1912. Synonymy by Girault, 1929: 14.

*nigrellus* Girault, 1911b: 282 (*Anaphes*), holotype ♀ (INHS) [1♀ paratype]. **TL:** USA, Illinois, Urbana, 26.vi.1909, in dish of xylol balsam in Natural History building, University of Illinois. Huber, 1992: 45 discussed the status of 2♀ and 1♂ specimens examined at the time of description, one of which was treated by Girault as a paratype. All three are lost.

*sinipennis* Girault 1911b: 280 (*Anaphes*), 3♀ syntypes (INHS), lost. **TL:** USA, Illinois, Urbana, 1.vii.1910, sweeping grass (2 syntypes), and Litchfield, 23.vii.1910, on stable window (1 syntype). Huber, 1992: 37 discussed the missing types.

##### **Neotropical Region**

*amplipennis* Oglöblin, 1962: 49 (*Anaphes* [*Austranaphes*]), holotype ♀ (MLPA) [1♂ paratype]. **TL:** Argentina, Neuquén, Pucará, Lago Lácar, 17.iii.1954.

*nunezi* Oglöblin, 1962: 51 (*Anaphes* [*Austranaphes*]), holotype ♀ (MLPA) [1♂ paratype]. **TL:** Argentina, Tierra del Fuego, Bahía Aguirre, 14.ii.1949.

*pucarobius* Oglöblin, 1962: 52 (*Anaphes* [*Austranaphes*]), holotype ♀ (MLPA) [1♂ paratype]. **TL:** Argentina, Neuquén, Pucará, Lago Lácar, 23.ii.1953.

*neuquenensis* Oglöblin, 1962: 54 (*Anaphes* [*Austranaphes*]), holotype ♀ (MLPA) [3♂ paratypes]. **TL:** Argentina, Neuquén, Pucará, Lago Lacar, 18.iii.1953. Synonymy by Huber, 1992: 53.

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TABLE 6. (Continued)

**Palearctic Region**

- arenbergi* Debauche, 1948: 166 (*Anaphes*), holotype ♀ (IRSNB) [2♀ paratypes]. **TL:** Belgium, Meerdael forest, 11.v.1941, on blueberry bushes in a pine copse.
- brevicornis* (Soyka, 1949: 316) (*Mymar*), holotype ♀ (NHMW); Soyka, 1955: 474 (transfer to *Ferrierella*). **TL:** Netherlands, Valkenburg, on window, 28.vi.1932.
- crassipennis* (Soyka, 1946a: 41) (*Mymar*), holotype ♀ (NHMW), redescribed by Soyka, 1949: 319; Soyka, 1955: 474 (transfer to *Ferrierella*). **TL:** Finland, Mosku at Luirojöki, forest meadow, 7.viii.1938 [Stammer legator].
- ferrierei* (Soyka, 1946b: 180) (*Mymar*), lectotype ♀ [#54] (NHMW), here designated to avoid confusion about the identity of the species [numerous paralectotypes, both sexes]. **TL:** Austria, Krössbach-Neustift, on window in hay stall, 12.ix.1946. **Syn. n.** Soyka (1946b) did not designate a holotype but only stated that he had numerous males and females in his collection; redescribed by Soyka, 1949: 315, who invalidly designated two holotypes, a female and a male, and specified that there were 50 paratypes. He also corrected the year of labelled the male specimen on slide #1113 as “gtype” [red label] and “genotype” [written on white label below species name] and “type” [red label]. Because *Anaphes* taxonomy is based on females, the female on slide #54 is designated as the lectotype; Soyka labelled it as a “para-type” [red label] and it is almost intact, with one antenna broken between fl<sub>3</sub> and fl<sub>4</sub>.
- cultripennis* Debauche, 1948: 162 (*Anaphes*), holotype ♀ (IRSNB) [4♀ paratypes]. **TL:** Belgium, Héverlé, 28.vi.1941, edge of ponds in the abbey of Parc. **Syn. n.**
- aries* Debauche, 1948: 168 (*Anaphes*), holotype ♀ (IRSNB) [4♀ and 1♂ paratypes]. **TL:** Belgium, Eegenhoven, 20.iv.1942, in marshy meadow. **Syn. n.**
- acutipennis* (Soyka, 1949: 315) (*Mymar*), holotype ♀ (NHMW) [5♀ paratypes]. **TL:** Finland, Luirojärvi, [20°E 69°10'N], 19.viii.1938, am Rasen oberhalb des Sees [on grass at upper part of lake] [Stammer legator]. **Syn. n.**
- pilosipennis* (Soyka, 1949: 328) (*Mymar*), holotype ♀ (NHMW). **TL:** Austria, Vienna, Leopoldsberg, 26.ix.1941 [Novicky legator]. **Syn. n.**
- sulphuripes* (Soyka, 1949: 330) (*Mymar*), holotype ♀ (NHMW). **TL:** Germany, Malchin, Jettchenhof, on window, viii.1935 [Stammer legator]. **Syn. n.**
- dilatatus* (Soyka, 1949: 342) (*Ferrierella*), holotype ♀ (NHMW). **TL:** Netherlands, Valkenburg, on window, 31.vi.1931 [25.vii]. **Syn. n.**
- laticornis* (Soyka, 1949: 345) (*Ferrierella*), holotype ♀ (NHMW), lost. **TL:** Netherlands, Valkenburg, 7.x.1931. Among Soyka's Valkenburg species, his *A. laticornis* description is closest to *A. luteicornis*. Both have the same wing width and the antennal proportions are almost identical. **Syn. n.**
- fennicus* (Soyka, 1955: 465) (*Mymar*), holotype ♀ (NHMW), lost [1♀ paratype, #53, in NHMW]. **TL:** Finland, Luirojärvi, [at river shore], 19.viii.1938 [Stammer legator]. **Syn. n.** The original description mentions only one specimen, the type. Therefore, the paratype is either the mislabelled holotype from the same locality but with a more detailed habitat description “am flussufer geketichert” [the handwriting is almost illegible but this seems to be what it says] and different date “27.Aug.1938” or it has no type status of any kind. Given the occasional differences in dates as recorded in Soyka's descriptions compared to the type slides themselves we suggest that the paratype may well be the holotype, particularly because the types of all the specimens collected by Stammer, and all but one of Soyka's other species were found so it seems unlikely that this holotype in particular would be missing.
- gracillimus* (Soyka, 1955: 466) (*Mymar*), holotype ♀ (NHMW). **TL:** Germany, Malchin, Jettchenhof, viii.1936 [Stammer legator]. **Syn. n.**
- luteicornis* (Soyka, 1955: 467) (*Mymar*), holotype ♀ (NHMW). **TL:** Netherlands, Valkenburg, 10.vi.1931. **Syn. n.**
- neoserenus* (Soyka, 1955: 469) (*Mymar*), holotype ♀ (NHMW). **TL:** Austria, Tirol, Neustift-Krössbach, 5.vii.1946 [on window]. **Syn. n.**
- serenus* (Soyka, 1955: 471) (*Mymar*), holotype ♀ (NHMW). **TL:** Germany, Malchin, Jettchenhof, [on window], viii.1936 [Stammer legator]. **Syn. n.**
- siegerfeldi* (Soyka, 1955: 472) (*Mymar*), holotype ♀ (NHMW). **TL:** Austria, Siegerfeld, 14.vii.1916 [Ruschka legator]. **Syn. n.**
- thoracicus* (Soyka, 1955: 473) (*Mymar*), holotype ♀ (NHMW). **TL:** Austria, Tirol, Krössbach, on window, 12.ix.1945. **Syn. n.**
- wertaneki* (Soyka, 1955: 474) (*Mymar*), holotype ♀ (NHMW). **TL:** Germany, Malchin, [on window], Jettchenhof, v.1935 [Stammer legator]. **Syn. n.**
- tarsalis* Mathot, 1969: 19 (*Anaphes*), holotype ♀ (IRSNB) [3♀ paratypes]. **TL:** Norway, Vassbygda, 15.viii.1965. **Syn. n.**
- ensipennis* (Soyka, 1949: 320) (*Mymar*), holotype ♀ (NHMW). **TL:** Netherlands, Valkenburg, on window, 18.vi.1931.
- flavipes* (Foerster, 1841: 45) (*Gonatocerus*), neotype ♀ (NHMW), designated by Samková *et al.*, 2017: 681; syntype(s?) ♀ (NHMW) destroyed, according to Soyka, 1949: 310; Foerster, 1847: 212 (transfer to *Anaphes*). **TL:** Germany, Aachen. Debauche 1948: 160 described a species under the name *flavipes* based on one specimen though he stated that he had several specimens collected in June from rushes from the edge of ponds in the abbey of Parc, Héverlé. He did not mention anything about type material. Considerable biocontrol literature has used this species name so rather than follow Debauche's concept, which might require a name change, a neotype is designated based on material reared from *Oulema melanopus* eggs collected on barley in the type locality. The leg colour varies from yellow (rare) to brown so colour cannot be used to distinguish the species from other species.

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TABLE 6. (Continued)

- auripes* Walker, 1846: 52 (*Anaphes*), lectotype ♀ (NMID), designated by Graham, 1982: 209. **TL:** England, almost certainly Southgate vicinity (Graham, 1982: 192). Synonymy by Samková *et al.*, 2017, 681.
- ciliatus* (Soyka, 1949: 317) (*Mymar*), holotype ♀ (NHMW). **TL:** Poland, Wiedenhof near Breslau, vii.1934. **Syn. n.**
- pilicornis* (Soyka, 1949: 326) (*Mymar*), holotype ♀ (NHMW); Soyka, 1955: 474 (transfer to *Ferrierella*). **TL:** Germany, Malchin [Jettchenshof], on window, viii.1935 [Stammer legator]. **Syn. n.**
- piliscapus* (Soyka, 1949: 327) (*Mymar*), holotype ♀ (NHMW). **TL:** Netherlands, Valkenburg, on window, 13.vi.1931 [18.vi]. **Syn. n.**
- spinosus* (Soyka, 1949: 330) (*Mymar*), holotype ♀ (NHMW). **TL:** Austria, Hundsheim, on window, 2.vii.1944 [Soyka legator] in description but Schlawe-See, 22.vii.1934 [Stammer legator] written on holotype slide. **Syn. n.** We invoke Article 73.1.2 (ICZN 1999) to correct the actual type locality to Poland, Schlawasee.
- varicolor* (Soyka, 1949: 350) (*Ferrierella*), holotype ♀ (NHMW). **TL:** Austria, Hundsheim, on mountain, 8.ix.1940 (in description and on one type slide so this is the real holotype) (10.ix on a second “type” slide; it has no status as a type specimen because it is not mentioned in the description). **Syn. n.**
- antoniae* (Soyka, 1955: 463) (*Mymar*), holotype ♀ (NHMW). **TL:** Netherlands, Valkenburg, 23.vii.1931 [25.vii]. **Syn. n.**
- elegans* (Soyka, 1955: 465) (*Mymar*), holotype ♀ (NHMW). **TL:** Netherlands, Valkenburg, on window, 15.x.1930. **Syn. n.**
- longispinosus* (Soyka, 1955: 467) (*Mymar*), holotype ♀ (NHMW). **TL:** Austria, Hundsheim, 18.ix.1940. **Syn. n.**
- mirabilis* (Soyka, 1955: 468) (*Mymar*), holotype ♀ (NHMW). **TL:** Poland, Ramischau near Breslau, vii.1933 [1934]. **Syn. n.**
- neospecialis* (Soyka, 1955: 469) (*Mymar*), holotype ♀ (NHMW). **TL:** Germany, Malchin, Jettchenshof [on window], viii.1936 [Stammer legator]. **Syn. n.**
- lemae* Bakkendorf, 1970: 153 (*Anaphes*), holotype ♀ (ZMUC) [32♀ and 10♂ paratypes (including those misidentified as *valkenburgica* by Bakkendorf, 1964: 3)]. **TL:** Poland, Lublin, 17.vi.1968, ex *Oulema* sp. Synonymy by Huber (1992: 48).
- fuscipennis* Haliday 1833: 346 (*Anaphes*), lectotype ♀ (NMID) designated by Graham, 1982: 207 [1♀ and 6♂ paralectotypes, but not explicitly designated as such by Graham, so their status is fixed here]. Walker (1846: 51) stated “common near London and in Ireland. **TL:** England, almost certainly Southgate vicinity (Graham, 1982: 192).
- pratensis* Förster 1847: 211 (*Anaphes*), lectotype ♀ (NHMW) designated by Huber 1992: 39 [1♂ paralectotype]. Förster’s description indicates that he also had at least 1 male specimen, which should be designated as a paralectotype if it is found. **TL:** Probably Germany, Aachen [according to Soyka (1949: 347) there was no locality or date on the specimen. Soyka collected a female of *A. pratensis* in Malkwitz (now Poland) in a field by a stream, v.1934, which may be the basis for his redescription. Förster’s original specimen (the lectotype) was on a minuton pin, and Soyka remounted it in Canada balsam. Synonymy by Graham 1982: 206; confirmed by Huber 1992: 38.
- neopratensis* (Soyka, 1946b: 182) (*Ferrierella*), holotype ♀ (NHMW), redescribed by Soyka, 1949: 339. **TL:** Austria, Hundsheim, Spitzerberg, [south side], 2.ix.1941 [Novicky legator]. Synonymy by Huber 1992: 38.
- capitulatus* (Soyka, 1949: 341) (*Ferrierella*), holotype ♀ (NHMW). **TL:** Netherlands, Valkenburg, on window, 31.vi.1931. Synonymy by Huber 1992: 38.
- filicornis* (Soyka, 1949: 343) (*Ferrierella*), holotype ♀ (NHMW). **TL:** Netherlands, Valkenburg, on window, 31.vii.1931. Synonymy by Huber 1992: 38.
- maculatus* (Soyka, 1949: 345) (*Ferrierella*), holotype ♀ (NHMW). **TL:** Netherlands, Valkenburg, [on window], 18.vi.1931. Synonymy by Huber 1992: 38.
- stammeri* (Soyka, 1949: 349) (*Ferrierella*), holotype ♀ (NHMW). **TL:** Poland, Breslau, Grueneiche, [Odland], in meadow, 23.ix.1934 [24] [Stammer legator]. Synonymy by Huber 1992: 38.
- gauthieri* Debauche, 1948: 171 (*Anaphes*), holotype ♀ (IRSNB) [1♀ and 1♂ paratypes]. **TL:** Belgium, Héverlé, 28.vi.1941, at the edge of pond in the abbey of Parc.
- flavus* (Soyka, 1949: 321) (*Mymar*), holotype ♀ (NHMW). **TL:** Germany, Malchin, Jettchenshof, on window, viii.1935 [1936] [Stammer legator]. **Syn. n.**
- leonhardwitzi* (Soyka, 1949: 324) (*Mymar*), holotype ♀ (NHMW). **TL:** Poland, Leonhardwitz near Breslau, ‘Oderwiesen’ [Oder River meadow], vii.1934. **Syn. n.**
- nigricornis* (Soyka, 1949: 325) (*Mymar*), holotype ♀ (NHMW). **TL:** Austria, Hundsheim, on window, [ex hay], 12.vii.1944. **Syn. n.**
- breviventris* (Soyka, 1949: 341) (*Ferrierella*), holotype ♀ (NHMW). **TL:** Netherlands, Valkenburg, on window, 2.x.1931. **Syn. n.**
- avalae* (Soyka, 1955: 464) (*Mymar*), holotype ♀ (NHMW). **TL:** Serbia, Avalaberg near Belgrade, viii.1934 [Stammer legator]. **Syn. n.**
- globosicornis* (Soyka, 1949: 322) (*Mymar*), holotype ♀ (NHMW). **TL:** Poland, Schlawasee, 2.vii.1934 [2.vii] [Stammer legator] in description but Austria, Hundsheim, on window, ex hay, 2.vii.1944 written on holotype slide [Soyka legator]. We invoke Article 73.1.2 (ICZN 1999) to correct the actual type locality to Austria, Hundsheim.
- medius* (Soyka, 1946a: 40) (*Synanaphes*), holotype ♀ (NHMW). **TL:** Austria, Hundsheim, on window, ex. hay, 7.vii.1943; redescribed by Soyka, 1949: 334, and male also described. Hellén (1974) suggested incorrectly that *medius* was the same as *fuscipennis*.

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TABLE 6. (Continued)

- ranalteri* (Soyka, 1946b: 181) (*Synanaphes*), holotype ♀ (NHMW); redescribed by Soyka, 1949: 333, where 10 ♀ paratypes invalidly added—these have no type status. **TL:** Austria, Tirol, Krössbach-Neustift, on window of hay stall, 12.ix.1945 [1946]. Synonymy by Huber 1992: 58.
- lacensis* (Soyka, 1949: 335) (*Synanaphes*), holotype ♀ (NHMW). **TL:** Austria, Burgenland, Jois am Neusiedlersee, 7.x.1941. Synonymy by Huber 1992: 58.
- intermedius* (Soyka, 1949: 344) (*Ferrierella*), holotype ♀ (NHMW). **TL:** Germany, Malchin, Jettchenhof, viii.1935 [1936] [Stammer legator]. **Syn. n.**
- pulchripennis* (Soyka, 1949: 348) (*Ferrierella*), holotype ♀ (NHMW). **TL:** Poland, Breslau, Gabitzstrasse [ulica Gajowicka], on window, viii.1933. **Syn. n.**
- speciosus* (Soyka, 1955: 472) (*Mymar*), holotype ♀ (NHMW). **TL:** Austria, Tirol, Krössbach, on window, 12.ix.1945. **Syn. n.**
- nipponicus* Kuwayama, 1932: 93 (*Anaphes*), numerous ♀ and ♂ syntypes (NIAES), lost? **TL:** Japan, Hokkaido, Ōno and Kagura (dates not given, but probably vi and vii.1931).
- ovipositor* (Soyka, 1946a: 41) (*Ferrierella*), holotype ♀ (NHMW), redescribed by Soyka, 1949: 346. **TL:** Germany, Malchin, Jettchenhof, on window, viii.1935 [1936] [Stammer legator].
- angustipennis* (Soyka), 1949: 339 (*Ferrierella*), holotype ♀ (NHMW). **TL:** Germany, Bavaria, Erlangen, caught in a fleichefalle [pitfall trap], no date [Stammer legator]. Name replaced with *A. germaniacus*. **Syn. n.**
- brevitarsis* (Soyka, 1949: 340) (*Ferrierella*), holotype ♀ (NHMW). **TL:** Germany, Malchin, Jettchenhof, on window, viii.1935 [Stammer legator]. **Syn. n.**
- tenuipennis* (Soyka, 1949: 350) (*Ferrierella*), holotype ♀ (NHMW). **TL:** Netherlands, Valkenburg, on window, vi.1932. **Syn. n.**
- quadraticornis* (Soyka, 1949: 329) (*Mymar*), holotype ♀ (NHMW). **TL:** Germany, Malchin, Jettchenhof, [on window], viii.1935 [Stammer legator].
- regulus* Walker: 1846: 52 (*Anaphes*), lectotype ♀ (NMID), designated by Graham, 1982: 208 [1♀ paralectotype, but not explicitly designated as such by Graham so its status is fixed here]. **TL:** England, almost certainly Southgate vicinity (Graham, 1982: 192). The paralectotype is illustrated in Thuróczy & O'Connor, 2015: 56, not the lectotype as incorrectly stated.
- autumnalis* Foerster, 1847: 212 (*Anaphes*), at least 1♂ and 1♀ syntypes (NHMW), destroyed, according to Soyka, 1949: 310. **TL:** Germany, probably around Aachen, in autumn in fields. Treated as a synonym of *regulus* by Graham, 1982: 208 and probably a variety of *flavipes* by Foerster, 1847: 212, but Debauche, 1948: 169 considered it a good species and Bakkendorf, 1971: 365 identified a specimen as this species reared from *Tipula* (Tipulidae) though it did not quite match Debauche's redescription. We accept Graham's synonymy.
- crassicornis* (Soyka, 1949: 318) (*Mymar*), holotype ♀ (NHMW); Soyka, 1955: 474 (transfer to *Ferrierella*). **TL:** Poland, Bruschewitz near Breslau, at a small lake, viii.1934. Name replaced with *A. soykai*. **Syn. n.**
- gracilior* (Soyka, 1949: 323) (*Mymar*), holotype ♀ (NHMW) [5♀ paratypes]. **TL:** Netherlands, Valkenburg, vii.1930. **Syn. n.**
- stygius* Debauche, 1948: 165 (*Anaphes*), holotype ♀ (IRSNB) [1♀ paratype]. **TL:** Belgium, Louvain, Kessel-Loo, 19.iv.1942, marshy meadow.
- wolfsthali* (Soyka, 1950: 120) (*Stammeriella*), holotype ♀ (NHMW). **TL:** Austria, Wolfsthal, Rehfeld, 27.ix.1941.
- germaniacus* Özdikmen, 2011: 839 (*Anaphes*). Replacement name for *A. angustipennis* (Soyka, 1949), not *A. angustipennis* Debauche, 1948. **Syn. n.**
- soykai* Özdikmen, 2011: 839 (*Anaphes*). Replacement name for *A. crassicornis* (Soyka, 1949), not *A. crassicornis* (Walker, 1846). **Syn. n.**

#### ANAPHES (PATASSON)

##### Afrotropical Region

*comosipennis* Girault, 1917: 17 (*Anaphes*), holotype ♀ (ZMHB). **TL:** Tanzania, no date or locality given.

##### Australian Region

*australia* (Girault, 1920: 97) (*Anaphoidea*), holotype ♀ (QM). **TL:** Australia, Queensland, Nelson, 5.iv.1919, on kitchen window.

*galtoni* (Girault, 1912: 152) (*Anaphoidea*), holotype ♀ (QM). **TL:** Australia, Queensland, Roma, 5.x.1911, sweeping vegetation along outskirts of town. [The single ♂ captured with the holotype (Girault 1914a: 288) has 1 transverse mps on flagellomere 1]. Assuming the sexes are conspecific, the species would have been classified in *A. (Yungaburra)* as defined by Huber (1992).

*inexpectatus* Huber & Prinsloo, 1990: 340 (*Anaphes*), holotype ♀ (ANIC) [10♀ and 14♂ paratypes]. **TL:** Australia, Tasmania, Hobart & Fingal, xi & xii.1988 [mixed laboratory culture from two localities].

*linnaei* (Girault, 1912: 153) (*Anaphoidea*), holotype ♀ (QM). **TL:** Australia, Queensland, Nelson, 9.vii.1912, on window.

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TABLE 6. (Continued)

- nitens* (Girault, 1928: 262) (*Anaphoidea*), lectotype ♀ (MVMA), designated by Huber & Prinsloo, 1990: 336 [several ♀ and ♂ paralectotypes (listed in Dahms, 1986: 348)]. **TL:** Australia, Victoria, Ferntree Gully, xi.1927.
- gonipteri* (Ferrière, 1930: 38) (*Anaphoidea*), lectotype ♀ (BMNH), designated by Huber & Prinsloo, 1990: 336 [21♀ and 15♂ paralectotypes]. **TL:** Australia, Victoria, Penola, ix.1926. Synonymy by Girault, 1930: 4.
- tasmaniae* Huber & Prinsloo, 1990: 338 (*Anaphes*), holotype ♀ (ANIC) [25♀ and 9♂ paratypes]. **TL:** Australia, Tasmania, Black Charles Opening, 4.xi.1987.

#### Nearctic Region

- calendrae* (Gahan, 1927: 32) (*Anaphoidea*), holotype ♀ (USNM) [123 paratypes, ♀ and ♂]. **TL:** USA, Missouri, Kirkwood, no date, ex *Sphenophorus* [as *Calendra*] *destructor* Chittenden.
- confertus* (Doutt, 1949: 155) (*Anaphoidea*), holotype ♀ (CAS). **TL:** USA, California, Napa Co., Oakville, 3.v.1948, sweeping native vegetation.
- conotrachelii* Girault, 1905: 220 (*Anaphes*), holotype ♂ (USNM) [20♀ and 19♂ paratypes]. **TL:** USA, Maryland, Arundel, 20.v.1905, ex *Conotrachelus nenuphar* (Herbst) (Curculionidae). Possibly same as *brevis*?
- cotei* Huber, 1997: 970 (*Anaphes*), holotype ♀ (CNC) [9♀ and 5♂ paratypes]. **TL:** Canada, Nova Scotia, Great Village, emerged 26.vii.1994 ex *Listronotus oregonensis* (LeConte) (Curculionidae) eggs in carrot pieces placed in carrot field from 27.vi–1.vii.1994.
- gerrisophaga* (Doutt, 1949: 156) (*Anaphoidea*), holotype ♀ (CAS) [1♀ paratype]. **TL:** USA, California, Shasta Co., Lake Britton, 29.vi.1947, ex *Gerris* sp. (Gerridae).
- listronoti* Huber, 1997: 963 (*Anaphes*), holotype ♀ (CNC) [57♀ and 24♂ paratypes]. **TL:** Canada, Quebec, Ste. Clotilde, 30.iv.1993, ex laboratory culture of *Listronotus oregonensis* (LeConte) (Curculionidae) on carrot.
- longiclava* (Doutt, 1949: 158) (*Anaphoidea*), holotype ♀ (EMEC) [1♀ paratype]. **TL:** USA, California, Morgan Hill, 2.vii.1947, sweeping native vegetation.
- pullicrurus* (Girault, 1910: 252) (*Anaphoidea*), holotype ♀ (INHS) [2♀ paratypes]. **TL:** USA, Illinois, Centralia, 26.viii.1909, on window.
- sordidatus* (Girault, 1909: 167) (*Anaphoidea*), lectotype ♀ (INHS), designated by Frison, 1927: 227 [1♀ and 2♂ paralectotypes, but the males lost (Huber *et al.*, 1997: 961)]. **TL:** USA, Illinois, Centralia, vi.1909, ex *Tyloderma foveolatum* (Say) (Curculionidae). Girault stated he had described the species from 3♀ and 5♂.
- victus* Huber, 1997: 967 (*Anaphes*), holotype ♀ (CNC) [52♀ and 68♂ paratypes]. **TL:** Canada, Quebec, Ste. Clotilde, viii.1994, 43<sup>rd</sup> generation ex laboratory culture of *Listronotus oregonensis* (LeConte) (Curculionidae) on carrot.

#### Neotropical Region

- atomarius* (Brèthes, 1913: 100) (*Anaphoidea*), holotype ♀ (MACN). **TL:** Argentina, General Urquiza, 1.xi.1912.

#### Palearctic Region

- angustipennis* Debauche, 1948: 184 (*Anaphes* [*Patasson*]), holotype ♀ (IRSNB). **TL:** Belgium, Louvain, Kessel-Loo, 19.iv.1942, marshy meadow next to drainage ditch.
- brevis* Walker, 1846: 52 (*Anaphes*), at least 1♀ syntype (BMNH), lost. **TL:** France, forest of Fontainebleau, vii.1830 (Walker 1846: 52 and Graham, 1982: 214).
- pectoralis* (Soyka, 1946b: 183) (*Hofenederia*), lectotype ♀ (NHMW), designated by Huber, 1992: 54 [numerous ♀ and ♂ paralectotypes]. **TL:** Austria, Hundsheim, on window, 2.vii.1944; female redescribed and male described by Soyka, 1949: 389. **Syn. n.** After the lectotype was designated a specimen with holotype (and genotype) labels by Soyka was found (NHMW) but because he did not indicate type status of any of his specimens of the type series in the original description the lectotype designation by Huber (1992) was justified. Both specimens have identical collection data.
- maculicornis* (Soyka, 1949: 390) (*Hofenederia*), holotype ♀ (NHMW) [30♀ paratypes]. **TL:** Austria, Krössbach, Neustift, Stubaital, on window, 11.viii.1945 [12.viii]. **Syn. n.**
- malchinensis* (Soyka, 1949: 392) (*Hofenederia*), holotype ♀ (NHMW). **TL:** Germany, Malchin, Jettchenhof, at window, viii.1935 [1936] [Stammer legator]. **Syn. n.**
- pinguicornis* (Soyka, 1949: 392) (*Hofenederia*), holotype ♀ (NHMW) [10♀ paratypes]. **TL:** Austria, Hundsheim, 10.x.1941. Synonymy under *pectoralis* by Huber 1992: 54. **Syn. n.** under *brevis*.
- rotundipennis* (Soyka, 1949: 394) (*Hofenederia*), holotype ♀ (NHMW). **TL:** Austria, Burgenland, Jois am Neusiedlersee, in grass, 7.x.1941. **Syn. n.**
- brunneus* (Doutt, 1949: 159) (*Anaphoidea*), holotype ♀ (EMEC) [3♀ paratypes]. **TL:** USA, California, Sonoma Co., Forestville, 16.iv.1947, sweeping native vegetation. **Syn. n.**
- latipterus* Boțoc, 1962: 111 (*Anaphes*), holotype ♀ (Boțoc collection), lost. **TL:** Romania, Cluj, Someș, vi.1959. **Syn. n.**
- maradonae* Jesu, 2003: 107 (*Anaphes*), holotype ♀ (DEZA) [1♀ and 3♂ paratypes]. **TL:** Italy, CS, Sibari, sandy beach, v.1995, ex Miridae in *Ephedra distachya* L. **Syn. n.**

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TABLE 6. (Continued)

- collinus* Walker, 1846: 52 (*Anaphes*), lectotype ♀ (NMID), designated by Graham, 1982: 212. Walker (1846) stated “found by Mr. Haliday on heath on a mountain.” **TL:** Northern Ireland (UK), Belfast, Cavehill, no date.
- pallipes* (Ashmead, 1887: 193) (*Alaptus*), holotype ♀ (USNM). **TL:** USA, Florida, Jacksonville, no date. **Syn. n.**
- relictus* (Soyka, 1949: 393) (*Hofenederia*), holotype ♀ (NHMW). **TL:** Austria, Hundsheim, 2.vii.1944. **Syn. n.**
- tenuis* (Soyka, 1949: 395) (*Hofenederia*), holotype ♀ (NHMW). **TL:** Austria, Hundsheim, on window, 12.vii.1944. **Syn. n.**
- aterrimus* (Soyka, 1949: 399) (*Fulmekiella*), holotype ♀ (NHMW) [10♀ paratypes]; Soyka, 1950: 121 (transfer to *Antoniella*). **TL:** Austria, Hundsheim, on window, 2.vii.1944. **Syn. n.**
- discolor* (Soyka, 1949: 404) (*Fulmekiella*), holotype ♀ (NHMW) [10♀ paratypes]; Soyka, 1950: 121 (transfer to *Antoniella*). **TL:** Austria, Hundsheim, on window [ex hay], 2.vii.1944. **Syn. n.**
- latus* (Soyka, 1949: 406) (*Fulmekiella*), holotype ♀ (NHMW) [5♀ paratypes]; Soyka, 1950: 121 (transfer to *Antoniella*). **TL:** Poland, Malkwitz near Breslau, in a field, v.1934. **Syn. n.**
- minor* (Soyka, 1949: 409) (*Fulmekiella*), holotype ♀ (NHMW) [5♀ paratypes]; Soyka, 1950: 121 (transfer to *Antoniella*). **TL:** Austria, Hundsheim, on window [ex hay], 2.vii.1944. **Syn. n.**
- nigerrimus* (Soyka, 1949: 410) (*Fulmekiella*), holotype ♀ (NHMW) [10♀ paratypes]; Soyka, 1950: 121 (transfer to *Antoniella*). **TL:** Austria, Hundsheim, on window [ex hay], 6.vii.1944. **Syn. n.**
- ornatus* (Soyka, 1949: 412) (*Fulmekiella*), holotype ♀ (NHMW) [10♀ paratypes; male was to be described later but never was]; Soyka, 1950: 121 (transfer to *Antoniella*). **TL:** Austria, Hundsheim, on window [ex hay], 2.vii.1944. **Syn. n.**
- ovatus* (Soyka, 1949: 413) (*Fulmekiella*), holotype ♀ (NHMW) [5♀ paratypes]; Soyka, 1950: 121 (transfer to *Antoniella*). **TL:** Poland, Malkwitz near Breslau, v.1934. **Syn. n.**
- pallidus* (Soyka, 1949: 414) (*Fulmekiella*), holotype ♀ (NHMW); Soyka, 1950: 121 (transfer to *Antoniella*). **TL:** Netherlands, Valkenburg, on window, 6.vi.1932. **Syn. n.**
- stubaiensis* (Soyka, 1949: 417) (*Fulmekiella*), holotype ♀ (NHMW) [50♀ and 51♂ paratypes]. **TL:** Austria, Krössbach-Neustift, Stubaital, on window in hay stall [ex hay] 15.vii.1945. Synonymy suggested by Graham 1982: 212; confirmed here. **Syn. n.**
- aestivus* (Soyka, 1950: 121) (*Antoniella*), holotype ♀ (NHMW). **TL:** Poland, Leonhardwitz near Breslau, ‘Oderwiesen’ [Oder River meadow], vii.1934. **Syn. n.**
- declinatus* (Soyka, 1950: 121) (*Antoniella*), holotype ♀ (NHMW). **TL:** Netherlands, Valkenburg, on window, vii.1932. **Syn. n.**
- discolorsimilis* (Soyka, 1950: 122) (*Antoniella*), holotype ♀ (NHMW). **TL:** Germany, Malchin, Jettchenhof, on window, viii.1935 [Stammer legator]. **Syn. n.**
- trijohanni* Jesu, 2002: 67 (*Anaphes*), holotype ♀ (DEZA) [at least 11♀ and 12♂ paratypes, and more in alcohol]. **TL:** Italy, Portici, 15.x.1991, ex *Curculio* sp. [handwritten footnote by author on reprint received] in *Eruca sativa*. **Syn. n.**
- crassicornis* (Walker, 1846: viii) (*Patasson*) and p. 52 (*Panthus*), lectotype ♀ (NMID), designated by Graham, 1982: 210 [possible paralectotypes 1♀ and 1♂; see Graham, 1982: 211]. **TL:** England, almost certainly Southgate vicinity (Graham, 1982: 192).
- lucidus* (Soyka, 1949: 370) (*Anaphoidea*), holotype ♀ (NHMW) [20♀ paratypes]. **TL:** Netherlands, Valkenburg, on window, 31[sic].vi.1931. **Syn. n.**
- serbiculus* (Soyka, 1949: 381) (*Anaphoidea*), holotype ♀ (NHMW). **TL:** Serbia, Andrejanica, viii.1934 [Stammer legator]. **Syn. n.**
- arcuatus* (Soyka, 1953a: 38) (*Anaphoidea*), holotype ♀ (NHMW). **TL:** Netherlands, Valkenburg, on window, 10.vii.1931. **Syn. n.**
- fortipennis* (Soyka, 1953b: 53) (*Anaphoidea*), holotype ♀ (NHMW). **TL:** Netherlands, Valkenburg, on window, 5.x.1930. **Syn. n.**
- longipilis* (Soyka, 1954: 60) (*Anaphoidea*), holotype ♀ (NHMW). **TL:** Poland, Breslau, Grüneiche, 24.ix.1933 [Stammer legator]. **Syn. n.**
- nemorosus* (Soyka, 1954: 60) (*Anaphoidea*), holotype ♀ (NHMW). **TL:** Poland, Leonhardwitz near Breslau, Oderwiesen [Oder River meadow], vii.1934. **Syn. n.**
- weidenhoferi* (Soyka, 1954: 62) (*Anaphoidea*), holotype ♀ (NHMW). **TL:** Poland, Weidenhof near Breslau, vii.1934. **Syn. n.**
- variatus* (Soyka, 1949: 384) (*Anaphoidea*), holotype ♀ (NHMW). **TL:** Germany, Malchin, Jettchenhof, viii.1935 [Stammer legator]. **Syn. n.**
- crassipilis* (Soyka, 1949: 360) (*Anaphoidea*), holotype ♀ (NHMW). **TL:** Poland, Breslau, Grueneiche, in meadow, 24.ix.1933 [Stammer legator].
- linearis* (Soyka, 1949: 407) (*Fulmekiella*), holotype ♀ (NHMW). **TL:** Poland, Neustadt, v.1934. **Syn. n.**
- crassus* (Soyka, 1953a: 38) (*Anaphoidea*), holotype ♀ (NHMW). **TL:** Austria, Tirol, Krössbach, on window, 24.vii.1945.
- stratipennis* (Soyka, 1954: 62) (*Anaphoidea*), holotype ♀ (NHMW). **TL:** Austria, Hundsheim, on window, [ex hay], 12.vii.1944. **Syn. n.**
- debilipennis* (Soyka, 1949: 361) (*Anaphoidea*), holotype ♀ (NHMW). **TL:** Netherlands, Valkenburg, on window, vi.1932 [Soyka legator] in description but Jettchenhof bei Malchin, on window, viii.1936 [Stammer legator] written on holotype slide. We invoke Article 73.1.2 (ICZN 1999) to correct the actual type locality to Germany, Malkin, Jettchenhof.

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TABLE 6. (Continued)

- superadditus* (Soyka, 1950: 123) (*Mariella*), holotype ♀ (NHMW). **TL:** Poland, Malkwitz near Breslau, in a field at a stream, v.1934. **Syn. n.**
- diana* (Girault, 1911a: 215) (*Anaphoidea*), lectotype ♀ (USNM) [1♂ paralectotype], designated by Schauff, 1984: 215. **TL:** England, London or vicinity?
- lameerei* Debauche, 1948: 182 (*Anaphes [Patasson]*), holotype ♀ (IRSNB) [25♀ and 3♂ paratypes]. **TL:** Belgium, Héverlé, 1.vi.1941. Synonymy by Schauff 1984: 214.
- apilosus* (Soyka, 1949: 356) (*Anaphoidea*), holotype ♀ (NHMW) [20♀ paratypes]; Soyka, 1950: 123 (transfer to *Mariella*). **TL:** Netherlands, Valkenburg, on window, 6.vi.1942 (original description). **Syn. n.** A [holo] type slide labelled as *Anaphoidea* crossed out in pencil and replaced with *Mariella* was seen but there is also a [holo] type slide, named as as *Mariella pilosa* and labelled Jettchenhof b[ei] Malchin, am fenster, viii.1936. A paratype ♀ (MHNG) with the Jettchenhof location was also seen, suggesting that the correct type locality is Jettchenhof. All three specimens are the same species.
- compressus* (Soyka, 1949: 360) (*Anaphoidea*), holotype ♀ (NHMW) [5♀ paratypes]; Soyka, 1950: 123 (transfer to *Mariella*). **TL:** Malchin, Jettchenhof, on window, viii.1935 [Stammer legator]. **Syn. n.**
- globosus* (Soyka, 1949: 366) (*Anaphoidea*), holotype ♀ (NHMW) [20♀ paratypes]; Soyka, 1950: 123 (transfer to *Mariella*). **TL:** Poland, Malkwitz near Breslau, in a field, v.1934. **Syn. n.**
- minimus* (Soyka, 1949: 371) (*Anaphoidea*), holotype ♀ (NHMW) [20♀ paratypes, one seen in MHNG]; Soyka, 1950: 123 (transfer to *Mariella*). **TL:** Netherlands, Valkenburg, on window, 6.vi.1932. **Syn. n.**
- parciventris* (Soyka, 1949: 376) (*Anaphoidea*), holotype ♀ (NHMW) [10♀? paratypes; one seen in MHNG]. **TL:** Netherlands, Valkenburg, on window, 6.vi.1931. **Syn. n.**
- reductus* (Soyka, 1949: 379) (*Anaphoidea*), holotype ♀ (NHMW) [5♀? paratypes; one seen in MHNG]; Soyka, 1950: 123 (transfer to *Mariella*). **TL:** Netherlands, Valkenburg, on window, 10.vi.1931. **Syn. n.**
- valkenburgicus* (Soyka, 1949: 385) (*Anaphoidea*), holotype ♀ (NHMW) [20♀? paratypes; one seen in MHNG]; Soyka, 1950: 123 (transfer to *Mariella*). **TL:** Netherlands, Valkenburg, on window, 10.vi.1931. **Syn. n.**
- niger* (Soyka, 1949: 411) (*Fulmekiella*), holotype ♀ (NHMW). **TL:** Austria, Hundsheim, 14.v.1942 [Bischoff legator]. **Syn. n.**
- heterotomus* (Mathot, 1969: 16) (*Patasson*), holotype ♀ (IRSNB). **TL:** Belgium, Hour, 6.vi.1965, sweeping. **Syn. n.**
- lineipennis* (Soyka, 1949: 368) (*Anaphoidea*), holotype ♀ (NHMW) [5♀ paratypes]. **TL:** Netherlands, Valkenburg, on window, 10.vi.1931.
- longipennis* (Soyka, 1949: 370) (*Anaphoidea*), holotype ♀ (NHMW). **TL:** Poland, Neustadt, in a field, v.1934. Synonymy suggested by Bakkendorf, 1960: 375 and 1964: 3; confirmed here. **Syn. n.**
- obscurus* (Soyka, 1949: 374) (*Anaphoidea*), holotype ♀ (NHMW) [holotype slide labelled as *Mariella*]; Soyka, 1950: 123 (transfer to *Mariella*). **TL:** Austria, Hundsheim, in a field, 17.v.1942 [Bischoff legator]. Synonymy suggested by Bakkendorf, 1960: 375; confirmed here. **Syn. n.**
- semimediatus* (Soyka, 1949: 381) (*Anaphoidea*), holotype ♀ (NHMW) [5♀ paratypes]; Soyka, 1950: 123 (transfer to *Mariella*). **TL:** Netherlands, Valkenburg, on window, 31.vi.1931. **Syn. n.**
- chrysomelae* (Bakkendorf, 1960: 372) (*Anaphoidea*), holotype ♀ (MHNG) [16♀ and 4♂ paratypes] [misspelled as *chrysomelinae* in Anonymous, 1961: 218] **TL:** Italy, Bocca di Magra, 22.iii.1959, ex *Chrysomela americana* L. (Chrysomelidae). **Syn. n.**
- dessarti* (Mathot, 1969: 18) (*Patasson*), holotype ♀ (IRSNB). **TL:** Belgium, Hour, 6.vi.1965. **Syn. n.**
- longicornis* Walker, 1846: 52 (*Anaphes*), lectotype ♀ (NMID), designated by Graham, 1982: 213 [6♀ and 6♂ paralectotypes]. **TL:** England, almost certainly Southgate vicinity (Graham, 1982: 192).
- fabarius* (Rondani, 1877: 180) (*Flabrinus*), lectotype ♀ (MZUF) designated by Bouček, 1974: 248. **TL:** Italy, probably around Parma, no date. **Syn. n.**
- archetti* Ghidini, 1945: 39 (*Anaphes*), lectotype ♀ (DEZA), designated by Huber, 2015: 33 [5 paralectotypes]. **TL:** Italy, Lazio, Latina, 13.v.1943, ex *Lixus junci* Boheman (Curculionidae). Synonymy suggested by Viggiani, 1994: 472; confirmed here. **Syn. n.**
- pannonicus* (Soyka, 1946a: 42) (*Anaphoidea*), holotype ♀ (NHMW); redescribed by Soyka, 1949: 376, where 10♀ paratypes invalidly added—these have no type status. **TL:** Austria, Hundsheim, on window, 7.vii.1943 [12.vii and ex hay]. **Syn. n.**
- leptoceras* Debauche, 1948: 187 (*Anaphes [Patasson]*), holotype ♀ (IRSNB) [1♀ and 1♂]. **TL:** Belgium, Héverlé, 4.vi.1941, clearings in woods. Questionable synonymy suggested by Graham, 1982: 213 and probably synonymy suggested by Viggiani, 1994: 472; confirmed here. **Syn. n.**
- additus* (Soyka, 1949: 354) (*Anaphoidea*), holotype ♀ (NHMW); Soyka, 1950: 123 (transfer to *Mariella*). **TL:** Austria, Hundsheim, on window, 2.vii.1944. **Syn. n.**
- communis* (Soyka, 1949: 358) (*Anaphoidea*), holotype ♀ (NHMW) [30♀? paratypes]. **TL:** Netherlands, Valkenburg, on window, 6.vi.1932. **Syn. n.**
- flavitarsis* (Soyka, 1949: 364) (*Anaphoidea*), holotype ♀ (NHMW) [10♀ paratypes]. **TL:** Austria, Tirol, Krössbach-Neustift, on window, 17.viii.1945. **Syn. n.**

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TABLE 6. (Continued)

- kressbachi* (Soyka, 1949: 367) (*Anaphoidea*), holotype ♀ (NHMW) [20♀ paratypes]. **TL:** Austria, Tirol, Krössbach-Neustift, Stubaital, on window, 24.vi.1945. **Syn. n.**
- longior* (Soyka, 1949: 369) (*Anaphoidea*), holotype ♀ (NHMW) [5♀ paratypes]. **TL:** Netherlands, Valkenburg, on window, 18.vi.1931. **Syn. n.**
- neoflavus* (Soyka, 1949: 372) (*Anaphoidea*), holotype ♀ (NHMW). **TL:** Austria, Tirol, Krössbach-Neustift, on window, 12.viii.1945. **Syn. n.**
- elongatus* (Soyka, 1949: 390) (*Hofenederia*), holotype ♀ (NHMW) [5♀ paratypes]. **TL:** Austria, Hundsheim, on window, 22.vii.1943. **Syn. n.**
- ater* (Soyka, 1949: 400) (*Fulmekiella*), holotype ♀ (NHMW) [10♀ paratypes]. **TL:** Austria, Hundsheim, on window, 2.vii.1944. **Syn. n.**
- balteatus* (Soyka, 1949: 401) (*Fulmekiella*), holotype ♀ (NHMW) [30♀ and ♂ paratypes; male was to be described later but never was]. **TL:** Austria, Hundsheim, on window, 12.vii.1944. **Syn. n.**
- campestris* (Soyka, 1949: 401) (*Fulmekiella*), holotype ♀ (NHMW) [30♀ and ♂ paratypes; male was to be described later but never was]. **TL:** Austria, Hundsheim, on window, 6.vii.1944. **Syn. n.**
- consimilis* (Soyka, 1949: 402) (*Fulmekiella*), holotype ♀ (NHMW) [30♀ and ♂ paratypes; male was to be described later but never was]. **TL:** Austria, Hundsheim, on window, 6.vii.1944 [2.vii]. **Syn. n.**
- dubius* (Soyka, 1949: 405) (*Fulmekiella*), holotype ♀ (NHMW) [30♀ and ♂ paratypes; male was to be described later but never was]. **TL:** Austria, Hundsheim, on window, 7.vii.1944 [2.vii]. **Syn. n.**
- malkwitzi* (Soyka, 1949: 408) (*Fulmekiella*), holotype ♀ (NHMW) [20♀ and ♂ paratypes; male was to be described later but never was]. **TL:** Poland, Malkwitz near Breslau, v.1934. **Syn. n.**
- longicornis* (Soyka, 1949: 407) (*Fulmekiella*), holotype ♀ (NHMW) [10♀ paratypes]. **TL:** Poland, Malkwitz near Breslau, in a field, v.1934. Name replaced with *A. eulongicornis*. **Syn. n.**
- pallidicornis* (Soyka, 1949: 415) (*Fulmekiella*), holotype ♀ (NHMW). **TL:** Austria, Hundsheim, on window, 2.vii.1944. **Syn. n.**
- rufus* (Soyka), 1949: 416 (*Fulmekiella*), holotype ♀ (NHMW) [30♀ paratypes; male was to be described later but never was]. **TL:** Austria, Krössbach-Neustift, Stubaital, 1100m, on window in a stable, 12.viii.1935. **Syn. n.**
- acutiventris* (Soyka, 1949: 419) (*Yungaburra*), lectotype ♀ (NHMW) [51♀ and ♂ paratypes]. Both sexes were described and a “type” designated for each. The female is therefore designated here as lectotype to avoid confusion about the identity of this species. **TL:** Austria, Krössbach-Neustift, Stubaital, on window, 7.viii.1945 [17.viii]. **Syn. n.**
- timidus* (Soyka, 1950: 124) (*Marielle* [sic]), holotype ♀ (NHMW). **TL:** Austria, Krössbach, Neustift, on window, 8.vii.1945. **Syn. n.**
- distinctus* (Soyka, 1953a: 38) (*Anaphoidea*), holotype ♀ (NHMW). **TL:** Netherlands, Sibbe near Valkenburg, in a sand pit, 20.vi.1932. **Syn. n.**
- duplicatus* (Soyka, 1953b: 53) (*Anaphoidea*), holotype ♀ (NHMW). **TL:** Austria, Hundsheim, on window, vii.1943. **Syn. n.**
- falsus* (Soyka, 1953b: 53) (*Anaphoidea*), holotype ♀ (NHMW). **TL:** Austria, Tirol, Krössbach, on window, 17.viii.1945. **Syn. n.**
- gabitzi* (Soyka), 1953b: 54 (*Anaphoidea*), holotype ♀ (NHMW). **TL:** Poland, Breslau, Gabitzstrasse [ulica Gajowicka], on window, viii.1933. **Syn. n.**
- medioacutus* (Soyka, 1954: 60) (*Anaphoidea*), holotype ♀ (NHMW). **TL:** Netherlands, Sibbe near Valkenburg, 20.vi.1932. **Syn. n.**
- neodistinctus* (Soyka, 1954: 60) (*Anaphoidea*), holotype ♀ (NHMW). **TL:** Austria, Hundsheim, on window, 2.vii.1944. **Syn. n.**
- piceicornis* (Soyka, 1954: 61) (*Anaphoidea*), holotype ♀ (NHMW). **TL:** Austria, Tirol, Krössbach, Neustift, on window, ix.1948. **Syn. n.**
- flavipennis* (Soyka, 1954: 64) (*Anaphoidea*). Described in key only. No type designated but holotype slide found (NHMW) and locality data taken from that. **TL:** Netherlands, Valkenburg, Ignatiuskolleg, on window, 28.vi.1932. **Syn. n.**
- sibbei* (Soyka, 1954: 64) (*Anaphoidea*). Described in key only, No type designated. But holotype slide found (NHMW) and locality data taken from that. **TL:** Netherlands, Sibbe near Valkenburg, 20.vi.1932, Sandgrabe (sic) [Sandgrube? = sand pit]. **Syn. n.**
- eulongicornis* Özdīmen, 2011: 839 (*Anaphes*). Replacement name for *A. longicornis* (Soyka, 1949), not *A. longicornis* Walker, 1846. **Syn. n.**
- luna* (Girault, 1914b: 109) (*Anaphoidea*), lectotype ♀ (USNM), designated by Huber, 2004: 24 [2♀ and 3♂ paralectotypes]. **TL:** Italy, Portici (introduced into USA, Utah, Salt Lake City, 8.iv.1911), ex *Hypera postica* (Gyllenhal) (Curculionidae).
- vulgaris* (Soyka, 1946a: 42) (*Anaphoidea*), holotype ♀ (NHMW), redescribed by Soyka, 1949: 386, where 20♀ paratypes invalidly added—these have no type status. **TL:** Netherlands, Valkenburg, on window, 10.vii.1932 [10.vi.1931]. **Syn. n.**
- hundsheimensis* (Soyka, 1946b: 184) (*Fulmekiella*), holotype ♀ (NHMW); redescribed by Soyka, 1949: 398, where 20♀ and ♂ paratypes were invalidly added—these have no type status. **TL:** Austria, Hundsheim, on window, 6.vii.1944. **Syn. n.**
- euryale* Debauche, 1948: 174 (*Anaphes* [*Patasson*]), holotype ♀ (IRSNB) [at least 1♀ and 1♂ paratypes]. **TL:** Belgium, Loverval forest, 7.iv.1942, grassy area. **Syn. n.**

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TABLE 6. (Continued)

- brachygaster* Debauche, 1948: 176 (*Anaphes [Patasson]*), holotype ♀ (IRSNB) [5♀ paratypes]. **TL:** Belgium, Héverlé, 4.vi.1941, tall grasses in humid area. **Syn. n.**
- devillei* Debauche, 1948: 177 (*Anaphes [Patasson]*), holotype ♀ (IRSNB) [2♀ and 3♂ paratypes]. **TL:** Belgium, Loverval forest, 10.viii.1941, on bushes. **Syn. n.**
- dorcas* Debauche, 1948: 179 (*Anaphes [Patasson]*), holotype ♀ (IRSNB) [3♀ paratypes]. **TL:** Belgium, Héverlé, 19.ix.1941, clearing in humid woods. **Syn. n.**
- albipes* (Soyka, 1949: 355) (*Anaphoidea*), holotype ♀ (NHMW). **TL:** Austria, Hundsheim, in a field, 6.vi.1942 [Bischoff legator]. **Syn. n.**
- differens* (Soyka, 1949: 363) (*Anaphoidea*), holotype ♀ (NHMW). **TL:** Austria, Hundsheim, [at window, ex hay and 2.vii], 7.vii.1944. **Syn. n.**
- neustadtii* (Soyka, 1949: 373) (*Anaphoidea*), holotype ♀ (NHMW). **TL:** Poland, Neustadt, in a field, v.1934. **Syn. n.**
- bicolor* (Soyka, 1953a: 38) (*Anaphoidea*), holotype ♀ (NHMW). **TL:** Austria, Hundsheim, on window, 8.vi.1942 [Bischoff legator]. **Syn. n.**
- aequipennatus* (Soyka, 1953a: 37) (*Anaphoidea*), holotype ♀ (NHMW). **TL:** Netherlands, Valkenburg, on window, 6.vi.1931. **Syn. n.**
- swiedecki* (Soyka, 1953b: 54) (*Anaphoidea*), holotype ♀ (NHMW). **TL:** Austria, Gumpoldskirchen, 3.ix.1941 [Novicky legator]. **Syn. n.**
- wratislawensis* (Soyka, 1954: 62) (*Anaphoidea*), holotype ♀ (NHMW). **TL:** Poland, Wiedenhof near Breslau, Scheitnig, [Oderwiesen (Oder river meadow)], 24.ix.1933 [Stammer legator]. **Syn. n.**
- palliditarsis* (Soyka, 1949: 375) (*Anaphoidea*), holotype ♀ (NHMW) [5♀ paratypes]. **TL:** Austria, Hundsheim, 2.vii.1944. **Syn. n.**
- ordinarius* (Soyka, 1954: 61) (*Anaphoidea*), holotype ♀ (NHMW). **TL:** Netherlands, Valkenburg, on window, 15.x.1930. **Syn. n.**
- speciosior* (Soyka, 1954: 61) (*Anaphoidea*), holotype ♀ (NHMW). **TL:** Austria, Hundsheim, 2.vii.1944, on window. **Syn. n.**
- pilosissimus* (Soyka, 1954: 61) (*Anaphoidea*), holotype ♀ (NHMW). **TL:** Poland, Oberschlesien, Neustadt, v.1934. **Syn. n.**
- maialis* Debauche, 1948: 185 (*Anaphes [Patasson]*), holotype ♀ (IRSNB) [1♀ and 1♂ paratypes]. **TL:** Belgium, Eeghenoven, 18.v.1942, along an irrigation ditch.
- semiflavus* (Soyka, 1949: 380) (*Anaphoidea*), holotype ♀ (NHMW) [5♀ paratypes]. **TL:** Netherlands, Valkenburg, on window, 6.vi.1932. **Syn. n.**
- devius* (Soyka, 1949: 403) (*Fulmekiella*), holotype ♀ (NHMW) [5♀ paratypes]. **TL:** Netherlands, Valkenburg, on window, 18.vi.1931. **Syn. n.**
- aequus* (Soyka, 1953a: 37) (*Anaphoidea*), holotype ♀ (NHMW). **TL:** Poland, Malkwitz near Breslau, v.1934. **Syn. n.**
- vulgarisimilis* (Soyka, 1954: 62) (*Anaphoidea*), holotype ♀ (NHMW). **TL:** Netherlands, Valkenburg, on window, 18.vi.1931. **Syn. n.**
- parallelipennis* (Soyka, 1949: 415) (*Fulmekiella*), holotype ♀ (NHMW). **TL:** Germany, Malchin, Jettchenhof, on window, viii.1935 [Stammer legator].
- rectipennis* (Soyka, 1949: 378) (*Anaphoidea*), holotype ♀ (NHMW). **TL:** Germany, Malchin, Jettchenhof, on window, viii.1935 [Stammer legator]. **Syn. n.**
- silesicus* (Soyka, 1946a: 42) (*Anaphoidea*), holotype ♀ (NHMW); redescribed by Soyka, 1949: 382, where 20♀ paratypes invalidly added—these have no type status. **TL:** Poland, Leonhardwitz near Breslau, vii.1934.
- calvescens* Debauche, 1948: 180 (*Anaphes [Patasson]*), holotype ♀ (IRSNB) [2♀ and 3♂ paratypes]. **TL:** Belgium, Héverlé, 28.vi.1941, tall grasses in humid areas, collected at the edge of pond in the abbey of Parc. **Syn. n.**
- brevior* (Soyka, 1949: 357) (*Anaphoidea*), holotype ♀ (NHMW) [20♀ paratypes]. **TL:** Netherlands, Valkenburg, on window, 6.vi.1931. **Syn. n.**
- exiguus* (Soyka, 1949: 363) (*Anaphoidea*), holotype ♀ (NHMW). **TL:** Germany, Malchin, Jettchenhof, on window, viii.1935 [Stammer legator]. **Syn. n.**
- flavicornis* (Soyka, 1949: 365) (*Anaphoidea*), holotype ♀ (NHMW) [5♀ paratypes]. **TL:** Netherlands, Valkenburg, on window, 6.vi.1931. **Syn. n.**
- pellucens* (Soyka, 1949: 377) (*Anaphoidea*), holotype ♀ (NHMW) [10♀? paratypes]. **TL:** Netherlands, Valkenburg, on window, 6.vi.1931 [1932]. **Syn. n.**
- similis* (Soyka, 1949: 383) (*Anaphoidea*), holotype ♀ (NHMW) [20♀? paratypes]. **TL:** Netherlands, Valkenburg, on window, 18.vi.1931. **Syn. n.**
- exiguosimilis* (Soyka, 1953b: 53) (*Anaphoidea*), holotype ♀ (NHMW). **TL:** Poland, Malkwitz near Breslau, v.1934. **Syn. n.**
- neobrevior* (Soyka, 1954: 60) (*Anaphoidea*), holotype ♀ (NHMW). **TL:** Poland, Neustadt, in a field, v.1934. **Syn. n.**
- obsoletus* (Soyka, 1954: 61) (*Anaphoidea*), holotype ♀ (NHMW). **TL:** Netherlands, Valkenburg, on window, 28.vi.1932. **Syn. n.**

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TABLE 6. (Continued)

*Nomina dubia*

- basalis* Förster, 1861: 42 (*Anaphes*), at least 1♀ syntype (NHMW), lost and most likely destroyed, according to Soyka 1949: 310. **TL:** Switzerland, likely Graubunden, possibly Rosegthal [Roseg Valley], viii or ix.1860.
- cinctus* (Soyka, 1949: 397, 398) (*Fulmekiella*). Described in key only. No type designated and no specimens located. **TL:** unknown.
- congener* Förster, 1861: 42 (*Anaphes*), at least 1♀ and 1♂ syntypes (NHMW), lost and most likely destroyed, according to Soyka 1949: 310. **TL:** Switzerland, likely Graubunden, possibly Rosegthal, viii or ix.1860.
- depressus* (Soyka, 1954: 63) (*Anaphoidea*). Described in key only but treated as though described previously, so possibly a *lapsus* for *compressus* Soyka. No type designated and no specimens located. **TL:** unknown.
- latipennis* Walker, 1846: 52 (*Anaphes*), holotype ♀ (?BMNH), lost. **TL:** France, Forest of Fontainbleau, presumably late vii.1830 according to Graham, 1982: 214. He stated that he was unable to recognize the species and the description is insufficient to identify it.
- parvus* (Foerster, 1841: 45) (*Gonatocerus*), at least 1♀ and 1♂ syntypes (NHMW), lost and most likely destroyed, according to Soyka 1949: 310. **TL:** Germany, Aachen vicinity. Because the female antennae were broken Foerster (1847) could not describe them. Yet in the original description he gave their colour as brown so they must have been broken off after description! Both Debauche, 1948: 183, and Hellén, 1974: 28 suggested that *A. parvus* might be the same as *lameerei* because Foerster's redescription seemed to fit that species well (especially the narrow wings) but Debauche then recommended the name be dropped, i.e., treated as a *nomen dubium*, because the antennal formula was not given and the species is not recognizable. We concur with Debauche.
- peyerimhoffi* (Kieffer, 1913: 101) (*Clinomyrmex*), at least 1♀ syntype (MNHN?), lost. **TL:** Algeria, Azerou Tidjer, near Tirourda Pass, Djurdjura massif [no collecting date], extracted from sifted debris.
- pulcher* (Soyka, 1949: 312) (*Mymar*). Described in key only. No type designated and no specimens located. **TL:** unknown.
- specialis* (Soyka, 1955: 462) (*Mymar*). Described in key only. No type designated and no specimens located. **TL:** unknown.

**Unavailable names**

- dytiscidarum* Rimsky-Korsakov, 1920: 7 (*Anaphes*). *Nomen nudum* (no description; see Triapitsyn, 2011: 26).
- nigroparva* (Soyka, 1954: 63) (*Fulmekiella*). *Nomen nudum* (no description).
- pallidipes* Soyka, 1949: 320 (no genus given). *Nomen nudum* (no description). Soyka stated that *ensipennis* is similar to/related with this name.

**Generic placement uncertain; fossil species doubtfully belonging in *Anaphes***

- schellwieniens* Meunier, 1901: 3 (*Anaphes*), holotype ♂ (MNHN?), lost. By tentative association with the female, this amber fossil described from a single male is probably also not an *Anaphes*; it may well be the opposite sex of *splendens*.
- splendens* Meunier, 1901: 3 (*Anaphes*), holotype ♀ (MNHN?), lost. This amber fossil described from a single specimen is very likely not an *Anaphes* on the basis of three described features: the fore wing has no marginal or medial space but rather uniform microtrichia beyond and behind the venation, the fore wing venation is almost half the length of the wing (Fig. 2 in Meunier (1901)), and the ovipositor is described as extending clearly beyond the posterior apex of the gaster. A Baltic amber female specimen, MCZ:Ent:Pale-18890 (MCZ), is labelled as *Anaphes splendens* but appears to have a 5-segmented funicle; otherwise it fits Meunier's description reasonably well. The large eye, in lateral view occupying most of the head, with gena extremely narrow for most of its length is remarkable.

**Nominal species transferred from *Anaphes* and its synonyms to other genera**

- bicolor* Dozier, 1932: 88. Transferred to *Schizophragma* Ogleblin by Huber, 1987: 834.
- cinctiventris* Girault, 1911b: 286. Transferred to *Erythmelus* Enock by Girault, 1929: 7.
- elongatus* Risbec, 1950: 623. Transferred to *Anagrus* by Ghesquière, 1951: 344.
- foersteri* Ratzeburg, 1848: 141. Transferred to *Anagrus* by Huber, 1992: 77. The species is better placed in *Erythmelus*, as *E. foersteri*, **comb. n.**, because the description states "... mit deutlich hervorstehendem dicken penis." [...] with clearly projecting thick penis], a characteristic of males of *Erythmelus* after death; they often extrude their genitalia especially when killed in ethanol.
- gracilipes* Girault 1916: 7. Transferred formally to *Erythmelus* by Girault, 1929: 7.
- gracilis* Howard, 1881: 370. Transferred to *Erythmelus* by Girault, 1929: 8.
- harveyi* Girault, 1912: 151. Transferred to *Erythmelus* by Huber, 1992: 77.
- himalayana* Mani & Saraswat, 1973: 101. Transferred to *Anagroidea* Girault by Subba Rao & Hayat, 1983: 131.

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**TABLE 6.** (Continued)

- kantii* Girault, 1912: 148. Transferred to *Erythmelus* by Girault, 1915b: 179.  
*laplacei* Girault, 1912: 150. Transferred to *Enaesius* Enock [= *Erythmelus*] by Girault, 1915b: 179.  
*latipennis* Crawford, 1913: 350. Transferred to *Schizophragma* by Ogloblin, 1949: 350.  
*mazzinini* Girault, 1915a: 164. Transferred to *Erythmelus* by Girault, 1915b: 179 (as *mazzinii*).  
*mellicornis* Ashmead 1887: 194. Transferred to *Amitus* Haldeman (Platygastriidae) by Gahan, 1927: 39.  
*ovivorus* Rondani 1870: 13. Transferred to *Telenomus* (Scelionidae) by Bouček, 1974: 273.  
*painei* Girault, 1912: 149. Transferred to *Erythmelus* by Girault, 1915b: 179.  
*picinus* Girault, 1916: 6. Transferred to *Erythmelus* by Girault, 1929: 8.  
*punctum* Shaw, 1798: 189. Transferred to *Camptoptera* by Huber, 2011: 55.  
*spinozai* Girault, 1913: 117. Transferred to *Enaesius* [= *Erythmelus*] by Girault, 1915b: 179.  
*tingitiphagus* Soares, 1941: 265 Transferred to *Erythmelus* by Huber, 1992: 77.  
*wallacei* Girault, 1912: 147. Transferred to *Enaesius* [= *Erythmelus*] by Girault, 1915b: 179.

Kalina (1989) mistakenly listed three names, *latissimus*, *pallidus*, and *rufoniger*, under *Anaphes* when in fact they were described in *Polynema* and are valid species in that genus. Kalina's mistake is evident because he cited Soyka's monograph on *Polynema*, published in 1956, not one of Soyka's papers on *Anaphes*, the last of which was published in 1955.

**Soyka's *Anaphes* collection, collecting methods, and habitats.** Soyka collected most of his specimens himself. Based on the published data Soyka also received 39 *Anaphes* specimens from four other collectors: H. Bischoff, S. Novicky, F. Ruschka and H.-J. Stammer. They sent Soyka, 4, 3, 1, and 31 specimens, respectively (from Stammer possibly also 5 paratypes each for *acutipennis* and *compressus*). For three species, *debilipennis*, *globosicornis*, and *spinosis* the published collecting locality differs completely from the locality written on the holotype slide (see Table 6) so the collector of *globosicornis* may have been Soyka (not Stammer, as published), and for *debilipennis* and *spinosis* the collector may have been Stammer (not Soyka, as published). Article 73.1.2 is invoked to clarify the type locality for these species (Table 6). Soyka had all the specimens mounted, uncleared, in Canada balsam on slides and he studied them at 200–300× magnification using a compound microscope. Although Soyka (1949) stated he had about 8000 specimens he also noted that lack of time prevented him from preparing them all. Later, Soyka (1955: 461) revised his estimate to over 10,000 specimens examined of *Mymar* group (his classification).

Soyka collected most of his own specimens from windows and explained how this was done in Valkenburg. The window(s) in question were on the uppermost floor of a house (Studienhaus) whose inner wall was covered with vines up to a height of 15 m; the “animals” (Tiere, in German) were wafted on wind currents from surrounding fields through an open window. For the Hundsheim specimens, Soyka would obtain hay from farmers around Hundsheim and place it in an abandoned back room of his residence, as illustrated in Triapitsyn (2010, figs 5, 6). The Malchin and Krössbach specimens were collected at the windows of a hay stall. Specimens collected from hay lofts (Neustift and Krössbach specimens) evidently originated from [alpine] hay fields. Soyka describe the latter type localities in various ways, depending on the species: Krössbach-Neustift, Krössbach, Neustift, or Neustift-Krössbach, sometimes with the valley name [Stubaital] or state [Tirol] also included. Most of the specimens sent to Soyka by others collectors were also from windows. The remaining specimens were collected otherwise, but either did not have a habitat mentioned or, for 18 species, were collected in the following habitats: on grass (*acutipennis*, *rotundipennis*), by pitfall trap [habitat not mentioned] (*angustipennis* Soyka), forest meadow (*crassipennis*), lake [lakeside presumably] (*crassicornis* Soyka), river/stream bank (*fennicus*), river meadow (*aestivus*, *leonhardwitzii*, *nemorosus*), sand pit (*distinctus*), field (*globosus*, *latus*, *longicornis* Soyka, *neobrevior*), field at stream (*superadditus*), meadow (*crassipilis*, *stammeri*), on mountain [presumably Hundsheimerberg, illustrated in Triapitsyn (2010, fig. 1)] (*varicolor*). Soyka concluded, not surprisingly, that the largest numbers of his species originated in fields.

**Soyka's type specimens.** We determined from Soyka's descriptions that he formally examined and designated as types about 900 *Anaphes* specimens, of which about 120 were in *A. (Anaphes)* and about 775 in *A. (Patasson)*. These consist of the primary types, and both validly and invalidly designated secondary types. Soyka described (in his descriptions, not including the six described in keys, four of which are treated as *nomina dubia*) 151 *Anaphes* species based on these specimens, objectively represented by 52 primary types in *A. (Anaphes)* (51 holotypes, 1 lectotype) and 99 primary types in *A. (Patasson)* (97 holotypes and 2 lectotypes). Soyka described *fennicus* from a single specimen but, interestingly, the type slide is labelled as a paratype; however, it almost certainly is the

holotype. We found in NHMW all the Soyka primary types except those of *laticornis* and the four *nomina dubia*: *cinctus* and *depressus* in *A. (Patasson)*, and *pulcher* and *specialis* in *A. (Anaphes)*. Luckily, all the holotypes and most of the paratypes are in NHMW. Soyka sent some paratypes to R. Doutt (EMEC) and C. Ferrière (MHNG) and perhaps to other institutions. In Soyka's collection almost 70 holotype slides of unpublished *Anaphes* nominal species were also found. He had placed these manuscript names in one or other of his genera. Their existence shows how much of a splitter Soyka was. Thankfully, most were never published! Those that were published are *cinctus*, *depressus*, *flavipennis*, *nigroparva*, *pulcher*, *sibbei* and *specialis* and are treated in various ways (Table 6).

In *A. (Anaphes)* 44 species were each described from a single specimen (the holotype). Three species had paratypes validly designated, all of them females unless otherwise stated (paratypes numbers in parentheses): *ferrierei* (~50, both sexes), *acutipennis* (5) and *gracilior* (5), for a total of 60. Paratypes (10) for *ranalteri* were designated subsequent to the original description so are invalid.

In *A. (Patasson)* 56 species were each described from a single specimen (54 holotypes, 2 lectotypes). Forty-two species had paratypes validly designated (their number in parentheses) for a total of about 670 specimens: *acutiventris* (51, both sexes, number of each not given), *apilosus* (20), *ater* (10), *aterrimus* (10), *balteatus* (30, both sexes, number of each not given), *brevior* (20), *campestris* (30, sex not given), *communis* (30, sex not given), *compressus* (5), *consimilis* (30, sex not given), *devius* (5), *discolor* (10), *dubius* (30, sex not given), *elongatus* (5), *flavicornis* (5), *flavitarsis* (10), *globosus* (20), *kressbachi* (20), *latus* (5), *lineipennis* (5), *longicornis* Soyka (10), *longior* (5), *lucidus* (20), *maculicornis* (30), *malkwitzi* (20, sex not given), *minimus* (20), *minor* (5), *nigerrimus* (10), *ornatus* (10), *ovatus* (5), *palliditarsis* (5), *parciventris* (20, sex not given), *pectoralis* (numerous, number and sex not given), *pellucens* (10, sex not given), *pinguicornis* (10), *rufus* (30), *reductus* (5, sex not given), *semiflavus* (5), *semimedium* (5), *similis* (20, sex not given), *stubaiensis* (101, including 51 males) and *valkenburgicus* (20, sex not given). When Soyka did not specify the sex of his paratypes we assume that most or all of them were females. He clearly indicated that he had males for 7 species, *balteatus*, *campestris*, *consimilis*, *dubius*, *malkwitzi*, *ornatus* and *rufus*, which he intended to describe later but never did. Paratypes for *hundsheimensis* (20), *pannonicus* (10), *silesicus* (20) and *vulgaris* (20) were designated subsequent to the original description so are invalid. Collection data for all of Soyka's *Anaphes* species are given in Table 6. Interestingly, Soyka (1955) also designated a "typisches stück" [“typical piece”, but not in the sense of a primary type] for *Ichneumon punctum* Shaw, since transferred to *Camptoptera* Förster by Huber (2011), and discussed why he did so.

**Soyka's *Anaphes* descriptions. A) Generic descriptions and keys to genera.** Soyka described seven new genera (six of them after people he knew) that are synonyms of *Anaphes*. Previous genera that Soyka redescribed briefly were *Anaphes*, which he incorrectly argued incorrectly should be given the name *Mymar*, *Anaphoidea* and *Yungaburra*. Soyka expanded the description of *Yungaburra* from Girault's two line diagnosis, but based on Soyka's own [European] species, *acutiventris*, which is not related to *nitens*, the type species of *Yungaburra*. Soyka's genera are based on trivial features that even he could not use consistently, as shown by his transfer of several of his species from one to another of his genera. Soyka produced two keys to genera, the first (Soyka 1949) with seven genera keyed to females (*Anaphoidea* and *Yungaburra* key out together as they are not separable) and four genera keyed to males (*Hofenederia* and *Synanaphes* not separable, *Ferrierella* and *Fulmekiella* not separable, and *Anaphoidea* and *Mymar* not separable); the second, to females only, with ten genera (Soyka 1955) though he could not distinguish two of them (*Anaphoidea* and *Yungaburra*).

**B) Species descriptions.** Soyka's eight papers containing *Anaphes* descriptions are fairly uniform in format. The 11 described species his 1946a and 1946b papers are redescribed again in his 1949 paper to follow the format of species described therein by adding relative measurements for the antennae and rewording and expanding the original descriptions. Comparison of the two descriptions and/or measurements for each of these species shows that they sometimes differ. To take only one example, the wing and antennal proportions of *A. crassipennis* differ, even though they were based on and therefore described from a single specimen: in Soyka (1946a) and in Soyka (1949), respectively, he gave the following proportions, among others: 1) fore wing  $4.5 \times$  as long as wide versus  $5 \times$  as long as wide; 2) longest fringe setae  $0.75 \times$  greatest wing width versus as wide as (in words) or  $35:40 \times$  [ $= 0.88 \times$ ] (in numbers) greatest wing width; 3)  $f_2$   $3 \times$  as long as  $f_1$  versus  $f_2$  more than  $2.5 \times$  as long as  $f_1$  (this “more than” could, of course, include  $3 \times$  as long). It should be noted that “länger als” [longer than] is not the same as “so lange wie” [as long as], i.e., the different phrases, regardless of language, give different results. If the measurements are converted into percentages this becomes evident. Thus, 300% ( $3 \times$ ) longer than 1 gives 4 whereas 300% (still  $3 \times$ ) as long as 1 gives 3. Soyka uses both phrases in his descriptions and we assume (and hope) that Soyka really meant

“as long as” in all cases. While the differences between the two descriptions may seem trivial many of his key features that lead to different species or groups of species are very slight differences in relative proportions of the fore wing or antenna. One possible explanation for the discrepancy in measurements is that the specimens moved slightly as the Canada balsam hardened during the three year gap between the first and second descriptions. One could simply disregard the original descriptions and use only his 11 redescriptions on the doubtful assumption that the latter are more correct but sometimes proportions are given in the original description but not in the redescription, so both descriptions must be taken into account. The accuracy of any of the proportions and relative measurements in the remainder of his species descriptions are therefore also suspect and Soyka’s measurements all need to be checked. Most are relative measurements, and in some cases it is clear that the measurements are double what they should be compared to other species because he evidently used a higher magnification objective lens. This was not stated in the relevant descriptions, i.e., those of *ensipennis*, *lacensis*, *malkwitzi*, and *rectipennis* (Soyka 1949), so if those measurements are to be compared with other species they must be halved.

Huber (1992) for *luna* in North America and Jesu (2001) for *trijohanni* in Italy, and others have shown that variation occurs between antennae on the same specimen, the relative proportions of the segment changing from one antenna with mps compared to the other antenna without or at least a different number of mps. They treated this as within the normal range of variation for the respective species. Even where the number of mps on both antennae is the same on each segment, the segment proportions may change, as illustrated here for *brevis* (Figs 36, 37), or apparently may change if both antennae are not oriented in perfect lateral view. At least 10 Soyka species, e.g., *aequipennatus*, *brevior*, *linearis*, show this intra-antennal variation and it is not clear from his descriptions which antenna he measured. In summary, and repeated here for emphasis, Soyka’s descriptions must be used with great caution, if they are used at all. Therefore their accuracy, let alone their usefulness are also in doubt.

The general format Soyka followed in each of his earlier species descriptions (Soyka 1946a, 1946b, 1949) was to describe colour (evidently based on slide mounted specimens only) followed or preceded by body parts—head, thorax, and abdomen (his terms), then appendages, i.e., fore wing and antennal descriptions and proportions, then total body length, type material and type locality. Legs were mentioned only with regard to their colour. Males were described for only six European species (*acutiventris*, *diana*, *ferrierei*, *medius*, *pectoralis*, *stubaiensis*). Soyka also added the description of the North American *conotrachelii*, which he included because Bakkendorf (1934) stated that he had reared *Anaphes* (as *Anaphoidea*) from eggs of *Agabus* sp. (Coleoptera: Dytiscidae) and unidentified eggs of Chrysomelidae in Denmark; Bakkendorf had listed all these reared specimens under *conotrachelii* (at least two species are likely involved, neither of them *conotrachelii*). Soyka named most of his species alphabetically in a given paper. In one way, Soyka (1950) was his best paper because he gave his specimen measurements in absolute terms (in mm), within each description. Descriptions in Soyka (1953a, b, 1954) are much briefer than previous descriptions because they contain no measurements within the descriptions. Instead, Soyka (1954) tabulated the absolute measurements (in mm) in considerable detail for the 26 *A. (Patasson)* species described in his 1953a, b, and 1954 papers. Unfortunately, he did not include *A. (Patasson)* species described in his previous papers (Soyka 1946a, 1946b, 1949, 1950) and of course could not have included those described later (Soyka 1955). Soyka (1949) included 19 illustrations in the introductory sections before any of his species descriptions. They are rather sketchy but fairly accurate line drawing of six fore wings, four female antennae, one male antenna, two scapes (one of the North American, *sordidatus*, consisting two views each of the male and female scape!) and six outlines of body habitus. Soyka described the 8 specimens received from Bischoff, Novicky, and Ruschka as 8 new species and the 31 specimens (possibly 41, it is not clear who collected the paratypes) received from Stammer as 31 new species. As noted above, many more of Soyka’s new species descriptions were also based on single specimens (Table 6). In *A. (Anaphes)* 22 species and in *A. (Patasson)* 65 species were described from specimens collected at windows. Contrary to the published type locality, however, the *spinosus* holotype slide has a lake [-side, presumably] as the habitat, not a window, but Soyka may have mixed up the collecting locality (as he did with *globosicornis*). Even when a long series of females was available it is clear that Soyka described each of his new species from one specimen only, almost certainly the holotype. The species described in each of his papers are listed below (valid species in bold), including the 13 that he transferred subsequently from one to another of his genera. We include, in brackets, the number and per cent that we consider valid—a total of 14 species.

Soyka (1946a)—6 spp. described as new: 3 in *Anaphes* (***medius***, *crassipennis*, *ovipositor*); 3 in *Anaphoidea* (*pannonicus*, *silesicus*, *vulgaris*) [4 species or 67% valid].

Soyka (1946b)—5 spp. described as new (order of genera given as published): in *Mymar* 1 (*ferrierei*); in

*Synanaphes* 1 (*ranalteri*); in *Ferrierella* 1 (*neopratensis*); in *Hofenederia* 1 (*pectoralis*); in *Fulmekiella* 1 (*hundsheimensis*) [0 species or 0% valid].

Soyka (1949)—95 spp. described as new (order of genera given as published; species listed alphabetically): in *Mymar* 16 described as new (*acutipennis*, *brevicornis*, *ciliatus*, *crassicornis* Soyka, *ensipennis*, *flavus*, *globosicornis*, *gracilior*, *leonhardwitzi*, *nigricornis*, *pilicornis*, *piliscapus*, *pilosipennis*, *quadraticornis*, *spinosus*, *sulphuripes*) and 2 redescribed (*ferrierei*, *crassipennis*); in *Synanaphes* 2 described as new (*lacensis*, *ranalteri*) and 1 redescribed (*medius*); in *Ferrierella* 13 described as new (*angustipennis* Soyka, *brevitarsis*, *breviventris*, *capitulatus*, *dilatatus*, *filicornis*, *intermedius*, *laticornis*, *maculatus*, *pulchripennis*, *stammeri*, *tenuipennis*, *varicolor*), and 3 redescribed (*neopratensis*, *ovipositor*, *pratensis*); in *Anaphoidea* 33 described as new (*additus*, *albipes*, *apilosus*, *brevior*, *communis*, *compressus*, *crassipilis*, *debilipennis*, *differens*, *exiguus*, *flavicornis*, *flavitarsis*, *globosus*, *kressbachi*, *lineipennis*, *longior*, *longipennis*, *lucidus*, *minimus*, *neoflavus*, *neustadtii*, *obscurus*, *palliditarsis*, *parciventris*, *pellucens*, *rectipennis*, *reductus*, *semiflavus*, *semimediuss*, *serbicu*, *similis*, *variatus*, *valkenburgicus*) and 5 redescribed (*conotracheli*, *diana*, *pannonicus*, *silesicus*, *vulgaris*); in *Hofenederia* 7 described as new (*elongatus*, *maculicornis*, *malchinensis*, *pinguicornis*, *relictus*, *rotundipennis*, *tenuis*) and 1 redescribed (*pectoralis*); in *Fulmekiella* 22 described as new (*aterrimus*, *ater*, *balteatus*, *campestris*, *consimilis*, *devius*, *discolor*, *dubius*, *latus*, *linearis*, *longicornis* Soyka, *malkwitzi*, *minor*, *nigerrimus*, *niger*, *ornatus*, *ovatus*, *pallidicornis*, *parallelipennis*, *rufus*, *stubaiensis*) and 1 redescribed (*hundsheimensis*); in *Yungaburra* 1 (*acutiventris*) [8 species or 9% valid].

Soyka (1950)—6 spp. described as new (order of genera as published; species listed alphabetically): in *Stammeriella* 1 (*wolfsthalii*); in *Antoniella* 3 (*aestivus*, *declinatus*, *discolorsimilis*); in *Mariella* 2 (*superadditus*, *timidus*) [1 species or 17% valid]. Soyka (1950: 123) also transferred 9 species from *Anaphoidea* to *Mariella*: *additus*, *apilosus*, *compressus*, *globosus*, *minimus*, *obscurus*, *reductus*, *semimediuss* and *valkenburgicus*.

Soyka (1953a)—in *Anaphoidea* 6 spp. described as new: *aequipennatus*, *aequus*, *arcuatus*, *bicolor*, *crassus*, *distinctus* [1 species or 17% valid].

Soyka (1953b)—in *Anaphoidea* 6 spp. described as new: *duplicatus*, *exiguosimilis*, *falsus*, *fortipennis*, *gabitzi*, *swiedecki* [0 species or 0% valid].

Soyka (1954)—in *Anaphoidea* 14 spp. described as new: *longipilis*, *medioacutus*, *nemorosus*, *neobrevior*, *neodistinctus*, *obsoletus*, *ordinarius*, *piceicornis*, *pilosissimus*, *speciosior*, *stratipennis*, *vulgarisimilis*, *weidenhoffi*, *wratislawensis* [0 species or 0% valid].

Soyka (1955)—in *Mymar* 15 spp. described as new: *antoniae*, *avalae*, *elegans*, *fennicus*, *gracillimus*, *longispinosus*, *luteicornis*, *mirabilis*, *neoserenus*, *neospecialis*, *serenus*, *siegerfeldi*, *speciosus*, *thoraciculus*, and *wertaneki*. [0 species or 0% valid]. Soyka (1955: 474) also transferred 4 species from *Mymar* to *Ferrierella*: *brevicornis*, *crassicornis*, *crassipennis*, and *pilicornis*. As stated already above, Soyka redescribed what he thought was *punctum* Shaw but Huber (2011) transferred this species to *Camptoptera*.

Soyka made brief comparisons with other species in only 11 of his species descriptions. Under *medius* Soyka compared *pratensis* and stated (English translations given) “from *pratensis* differs through the thicker and shorter funicle segments”. Under *crassicornis* [= *soykai*] Soyka stated “related to *pulcher* and *gracilior*.” Under *crassipennis* Soyka stated “related with *pulcher*.” Incidentally, *pulcher* was a name keyed twice but not described under that name so its identity is a mystery; the name is treated as a *nomen dubium* (Table 6). Under *ensipennis* Soyka stated “related with *pallidipes*” [a name that is not keyed or described]. Under *globosicornis* Soyka stated “related with *breviventris*, *leonhardwitzi* and *brevitarsis*.” Under *leonhardwitzi* Soyka stated “related with *brevitarsis* and very similar to *nipponicus*.” The latter species, described from Japan (Kuwayama 1932), is represented by several reared, slide-mounted specimens (CTKH) in poor condition evidently sent by Kuwayama to Germany and which Soyka presumably saw. Although Kuwayama identified these specimens they are, unfortunately, not part of the original type series because they were reared at a different locality from the type series and at a later date (Samková *et al.* 2017). Under *nigricornis* Soyka stated “related with *leonhardwitzi*.” Under *piliscapus* Soyka stated “a sure/certain similarity with *crassicornis* and *ensipennis*.” Under *spinosus* Soyka stated “a sure/certain similarity with *sulphuripes*.” Under *capitulatus* Soyka stated “the antenna is similar to *filicornis*.” Under *tenuis*, the only species in *A. (Patasson)* with a comparison, Soyka stated “ovipositor far exserted, related with *reicta*.” Clearly, Soyka made different and evidently contradictory or at least non-compatible comparisons in different places. Regardless, except for *tenuis*, he did not mention any morphological features that might indicate in each case how the species compared were similar.

Regarding variation, Soyka (1949: 306) stated that “the value, constancy and breadth of variation of these characters will be dealt with more fully. Since these characters are very variable [Soyka admitted this!] these will be addressed accordingly in the keys”. As shown below, Soyka did indeed key out some nominal species more than once but we repeat emphatically that he still greatly underestimated intraspecific variation and didn’t really follow up on his own statement about variability.

**Soyka’s keys to species.** Just as his *Anaphes* descriptions must be used carefully, Soyka’s identification keys must be used with great caution, if at all. When keying out a slide-mounted specimen a species name will always be reached in one or other of his keys but that does not mean much, given Soyka’s species concepts. For example, Bakkendorf (1960) keyed his new species *chrysomelae* through Soyka’s (1949) key to *Anaphoidea*, and arrived at four names, *longipennis*, *lineipennis*, *semimediuss* and *obscurus*, that matched the features of *chrysomelae*. We agree that the first two are clearly synonyms of *chrysomelae* but we are less certain about the last two, though we still synonymized them under *lineipennis*—all have an ovipositor distinctly shorter than the metatibia, however. Bakkendorf did not have access to Soyka’s types or see any photographs so the fact that he managed to associate correctly two of the Soyka’s species with *chrysomelae* is remarkable. We based our decisions on photographs of the holotypes of all four of these Soyka names. Another problem, as discussed above for some Soyka specimens, is that depending on which antenna is measured the same specimen might key out to two different places in his keys because of variation between antennae of the same specimen.

There are no keys in Soyka (1946a, b). There are five keys in Soyka (1949): the *Mymar* key contains 26 couplets leading to 21 species, including one name, *pucher*, that occurs twice in that key (*pulcher* is therefore available; ICZN 1999, Article 13.1.1) and was also mentioned twice under two different described species, *crassicornis* [= *soykai*, a replacement name] and *crassipennis*; the *Ferrierella* key contains 17 couplets leading to 15 species; the *Anaphoidea* key contains 36 couplets leading to 36 species; the *Hofenederia* key contains 8 couplets leading to 8 species; and the *Fulmeikiella* key contains 22 couplets leading to 21 species, including one name, *cinctus*, that appeared twice in the *Fulmeikiella* key but nowhere else (*cinctus* is available, however). There are two keys in Soyka (1950): the *Antoniella* key contains 18 couplets to 11 species; the *Mariella* key contains 9 couplets to 10 species. There are no keys in Soyka (1953a, b). There is one key in Soyka (1954); it contains 69 couplets leading to 59 species of *Anaphoidea* including four names, *depressus*, *flavipennis*, *nigroparva* and *sibbei* that appear in that key and nowhere else. Three are described and therefore available but one, *nigroparva*, is definitely a *nomen nudum* because the second half of couplet 16 states “... schwartzovibraunes Tier ... (cf. *Fulmeikiella nigroparva*), Soyka”; we interpret this literally and strictly to mean that this part of the couplet describes an unmentioned species that Soyka compares with (cf. or confer in Latin = compare in English) *nigroparva*; *nigroparva* itself is not actually described at all so we are justified in treating it as an unavailable name. Interestingly, but confusingly, Soyka used exactly the same construction in couplets 17 (*hundsheimensis*), 23 (*acutiventris*), 51 (*longipilis*) 60 (*flavipennis*) and 52 (*nemorosa*) but because those species were described elsewhere they are available names. There is one key in Soyka (1955); it contains 44 couplets to 31 species of *Mymar*; one species, *specialis*, appears in that key but nowhere else (it is available, however), and *punctum* belongs in *Camptoptera* (Huber 2011).

No type designations were made for any of the six available Soyka species names (*cinctus*, *depressus*, *flavipennis*, *pulcher*, *sibbei*, and *specialis*) that were described only in keys (Soyka 1949, 1954). Type slides for *sibbei* and *flavipennis* were found in NHMW so type localities for these names are therefore known; those two types apparently belong to the same species and are treated as synonyms of *longicornis* Walker (Table 6). Because no type material was found for the other four we are not sure what the species are so we treated them as *nomina dubia* (Table 6).

Several species keyed out twice or more in a given key, illustrating that Soyka treated variation within species to some extent in the keys if not in the descriptions: in the 1949 *Mymar* key *crassicornis*, *gracilior*, *leonhardwitzii*, *pulcher*, *spinosus* and *sulphuripes* each come out twice; in the *Ferrierella* key *breviventris*, *maculatus*, and *varicolor* each come out twice; in the *Hofenederia* key *relictus* comes out twice; and in the *Fulmeikiella* key *cinctus* comes out twice. In the 1950 *Antoniella* key *discolor*, *declinatus*, *latus*, *nigerrimus* and *ovatus* each come out twice. In the 1954 *Anaphoidea* key *distinctus*, *flavipennis*, *kressbachi*, *longipilis*, *nemorosus*, *palliditarsis* and *weidenhoferi* each come out twice and *medioacuta* comes out three times. In the 1955 *Mymar* key *avalae*, *elegans*, *fennicus*, *gracilior*, *leonhardwitzii*, *neospecialis*, *siegerfeldi*, *spinosus*, *sulphuripes*, *thoracicus* and *wertaneki* each come out twice, and *luteicornis* comes out three times.

Although Soyka evidently recognized some variation in some of his species, which reduced the number he might have described, this is still greatly offset by the numerous nominal species that he did describe and many more he could have described, as discussed above. Two examples are given: for *collinus* in *A. (Patasson)* and *fuscipennis* in *Anaphes* (*Anaphes*). *Anaphes collinus* has 16 synonyms, 14 of which are Soyka names (Table 6). Soyka keyed these out as follows (names in each key given chronologically, in the order listed in Table 6). In his key to *Hofenederia* species (Soyka 1949: 388): *relictus* in couplets 6 and 8 and *tenuis* in couplet 8. In his key to *Fulmekiella* species (Soyka 1949: 397): *aterrimus* in couplet 12, *discolor* in couplet 11, *latus* in couplet 4, *nigerrimus* in couplet 13, *ornatus* in couplet 9, *ovatus* in couplet 4, *pallidus* in couplet 6, and *stubaiensis* in couplet 7. In his key to *Antoniella* species (Soyka 1950: 122): *aterrimus* in couplet 15, *discolor* in couplets 10 and 14, *latus* in couplets 2 and 6, *minor* in couplets 8 and 16, *nigerrimus* in couplet 13, *ornatus* in couplet 5, *ovatus* in couplets 2 and 17, *pallidus* in couplet 12, *stubaiensis* in couplet 9, *aestivus* in couplets 16 and 18, *declinatus* in couplets 10 and 14, and *discolor similis* in couplet 8. Thus, *minor* was not in his *Fulmekiella* key, though he had placed this species originally in *Fulmekiella*, but instead it appeared for the first time in his *Antoniella* key. Eight of his species were keyed out twice, either in the same key: *relictus* in *Hofenederia*, and *aestivus*, *declinatus*, *latus*, *minor*, *nigerrimus*, and *ovatus*, in *Antoniella*, and/or in different keys (both *Fulmekiella* and *Antoniella*): *discolor*, *latus*, *nigerrimus*, *ornatus*, *ovatus*, *pallidus* and *stubaiensis*. The reason for some of these duplications is that Soyka transferred some of the species from one genus to another and therefore keyed the species out again in the new genus. It turns out that eight of the nominal species in Soyka's *Ferrierella* key of 22 couplets and every single one of the nominal species in his *Antoniella* key of 18 couplets is actually one and the same species, namely *collinus*. This example looks worse than it is because several of the species were keyed out in both keys.

*Anaphes fuscipennis* has six synonyms, one of which is a Förster name and five of which are Soyka names (Table 6). All six synonyms are keyed in the first 8 couplets of his 17 couplet *Ferrierella* key (Soyka 1949: 337). One name, *maculatus*, is keyed twice, which is interesting because that species was described from only one specimen, as were all the others synonymized under *fuscipennis*. Soyka even provided an accurate line drawing of the female antenna of *pratensis*, one of the synonyms of *fuscipennis* which is arguably the most distinct species in *Anaphes*, yet he failed to notice that all six names had essentially identical antennae. Instead, Soyka used trivial features of body colour and relative proportions of flagellar segments or fore wing to distinguish his species.

In various places in Soyka's keys, the couplets are not always rigorously contrasting, e.g., in his *Fulmekiella* key (Soyka 1949: 397) *linearis* is distinguished from *parallelipennis* as follows (English translation given):  $fl_4$  clearly shorter than  $fl_5$ , scape shorter than width (*linearis*) versus  $fl_4$  as long as or slightly longer than  $fl_5$ , scape as long as clava (*parallelipennis*). The scape feature is useless to distinguish the two species because it is described completely differently in the alternate half of the couplet. In any case, the first phrase is incorrect because the scape in females of *Anaphes* (and other Mymaridae) is not shorter than its width. Usually, however, couplet features are rigorously contrasting but are so finely divided that what Soyka is keying is individual specimens not species, and most of the couplets simply reflect variation among individuals.

Soyka made heavy use of colour and proportions, almost exclusively of wings and female antenna, to describe his *Anaphes* species but listed various other features as well (Soyka 1949: 305). He also did this in his keys as he explained a few pages further on (Soyka 1949: 310). Although Soyka placed considerable emphasis on body colour in his descriptions it is obvious from examination of his type slides that colour variation among the types is due at least in part to slightly different clearing of specimens that occurred after having been mounted in Canada balsam. Luckily, he used colour only slightly in his keys even though he may have decided he had a new species based first on slight colour differences.

Six species names appeared only in keys (Soyka 1949, 1954). Although the features mentioned for five of these—*cinctus*, *flavipennis*, *pulcher*, *sibbei*, and *specialis*—constitute descriptions, no type designations were made for any of them. Type slides for *sibbei* and *flavipennis* were found in NHMW so type localities for these names are therefore known; those two types apparently belong to the same species and are treated above as synonyms of *longicornis* Walker. The name *pulcher* was used twice in a key (Soyka 1949: 312) and mentioned twice under two different described species, *crassicornis* [= *soykai*, a replacement name] and *crassipennis* but was itself not described, at least not using the name *pulcher*. Because no type material was found and we are not sure what this species is we treat it as a *nomen dubium*. Another species name, *nigroparva*, was used once in a different key (Soyka 1954: 63) but without description. Soyka was evidently referring to a previous description under some other name but cited it incorrectly. We are justified in treating *nigroparva* as an unavailable name.

**Species characters in *Anaphes* as used by various authors.** Walker (1846: 52), quoting Haliday, stated “the species [of *Anaphes*] are all difficult to characterize: their colours are much alike, but the length of the tarsal joints and of the antennae may be compared.” Haliday was certainly a careful observer to note such features, particularly tarsomere length, on specimens of the single *Anaphes* species he described (Fig. 87) and presumably on other specimens he must have examined, some of which were later described by Walker. We suggest that not too much in the way of good characters has been added to distinguish reliably the various species of *Anaphes* since Haliday (1833), about 170 years ago. Almost all characters used to distinguish species in *Anaphes* are still quantitative and therefore continuous. If, apparently, a discrete gap occurs, the range of numerical values provided may simply be an artifact of measuring too few specimens of a given species, regardless of the measurements or ratios selected. Measuring more specimens may show that the intraspecific variation between two apparent “species” actually overlaps for the features measured. Thus, deciding where the differences between two species occur is arbitrary if only those measurements are used to define the species. Ratios are more useful than absolute measurements because overall size differences among specimens within a species are factored out. Conversely, differences in measurements or ratios within a single species may also be due to rearing from different hosts and the gap in measurements of specimens reared from one or other host may indeed be discontinuous, as proved experimentally for *iole* on eggs reared from two species of Miridae (Huber & Rajakulendran 1988) or the largest and smallest specimens from a series of related hosts have measurements that do not necessarily overlap, e.g., in *calendrae* (Gahan 1927; Huber 2006). Because almost all *Anaphes* species, whether those of Soyka or of other authors, were described from five or fewer specimens it is clear that most of the species are not well circumscribed on the basis of relative or absolute measurements or ratios.

Most authors also used colour to some extent in their *Anaphes* descriptions. Unfortunately, *Anaphes* specimens are mostly uniformly black or brown but may appear variable because of their age and state of preservation (those preserved in ethanol fade from black to brown over time, unless kept in a freezer), as well as the mounting medium (almost always Canada balsam) so colour is almost useless in defining species. However, colour pattern, especially of the fore wing margin compared to the central area of the wing, and sometimes of the legs, may occasionally be reliable and useful for distinguishing some species.

**a) Continuous characters.**

1) Fore wing: length and width, and ratios of length to width. Used by Debauche (1948), Soyka and Huber (all their papers), and others.

2) Female antenna: segment length and width, and sometimes ratios of length to width. Used by Soyka and Huber (all their papers); Debauche (1948) used lengths only.

3) Male genitalia: ratios of various parts. Used by Viggiani (1994).

4) Metatarsomeres: ratio of length of segments 1 and 2. Used occasionally; usefulness of their relative lengths first noticed by Haliday (1833). Other authors used them but not consistently. Soyka did not use them at all, stating that “legs offer few useable characters” (Soyka 1949: 306). The relative proportions of metatarsomeres 1 and 2 are indeed useful characters. The best way to measure their length accurately is from one tarsal insertion to the next and, for tarsomere 1, from its junction with the metatibia.

5) Ovipositor: length, and ratio either compared to gaster length (Soyka used this) or to metatibia length (Huber used this); also whether the ovipositor projects posteriorly beyond the gastral apex and/or anteriorly under the mesosoma (measured as extending forward to apex or base of meta-, meso- or procoxa). Used by most authors.

6) Body length: used by all authors but body length is variable depending on whether the specimen is air dried or critical point dried on a point or card, or cleared or uncleared and slide mounted, and whether the metasoma is in line with mesosoma or not.

7) Mesosoma: length (and width). Soyka used this, often to define his new genera but although he stated that he used width almost all his specimens are oriented in lateral view so he could hardly have measured mesosoma width unless he did so before slide-mounting, which seems unlikely. He certainly did not give numerical length/width ratios in his descriptions. If used at all, mesosoma length is perhaps best used in comparison with gaster length.

**b) Qualitative or discrete characters.**

1) Number of claval segments in females. In Debauche’s subgeneric classification, one in *A. (Anaphes)* or two in *A. (Patasson)*.

2) Number of flagellar segments in males. Apparently 10 in *A. (Anaphes)* and 11 in *Anaphes (Yungaburra)*.

Debauche (1948: 154) observed the very small (anelliform)  $fl_1$  in all *Anaphes* males of both of his subgenera and realized astutely that they all actually have 11 segments. Huber (1992) noted that the anelliform  $fl_1$  of males had 1 mps or a trichoid seta in *A. (Yungaburra)* but not in *A. (Anaphes) sensu* Huber.

3) Number and distribution of mps on the funicle segments in females. This is important for characterizing the species, but host-induced variation is known (Huber & Rajakulendran 1988). A funicle segment is wider if it has mps and narrower if it doesn't and even the length may vary. Interestingly, there is almost no variation in mps number on  $fl_1$  [always 0 in *A. (Anaphes)* species but often with 1 in *A. (Yungaburra)* species], and  $fl_5$  and  $fl_6$  [always 2 on each, with one exception found in two specimens (BMNH) of *fuscipennis* where  $fl_5$  had 0 mps]; intraspecific variation among specimens occurs almost entirely on  $fl_2$  and  $fl_4$  and to a lesser extent on  $fl_3$ . For a given segment a single specimen may even have a different number of mps on each antenna (0 and 1, 1 and 2, or 0 and 2). Soyka did not use mps presence and distribution at all but several other authors did.

4) Direction of occipital groove. Either this forms a straight line with the supraorbital trabecula and is directed ventrally (Fig. 4; Huber 2006, fig. 30), or it forms an abrupt angle with the trabecula and is directed medially towards the occipital foramen (Fig. 33; Huber 2006, figs 31, 32).

5) Presence or apparent absence of cross-striations on surface of scape. Soyka used this feature a great deal, even as a reason to propose new genera, but because only the inner (medial) surface has these, if he observed the outer (lateral) surface he would have missed seeing the cross striations.

6) Shape of fore wing. This is difficult to describe qualitatively but it is an important character. Soyka, Debauche and Huber used fore wing shape, particularly the shape of the wing apex.

7) Number of longitudinal lines of microtrichia on fore wing. Girault (1929), Soyka (most papers) and Debauche (1948) used this, but it is difficult to determine how they counted the lines, especially because both dorsal and ventral surfaces of the wing have them.

8) Length of marginal space (the narrow bare area distal to venation) compared to length of veins. Girault (1929: 14) was the first to use this feature (only once, to identify *hercules*), and Soyka was the first to give it a name and used it often.

9) Number and type of sensilla on underside of female clava. Used only by Baaren *et al.* (1999).

10) Setae on body and antenna. Position of the setae on fore wing venation, and thickness, length and density of setae on female antenna. These features are difficult to describe accurately. Debauche and Soyka both made use of setae but not in their species keys, though Debauche carefully illustrated the wing venation setae. Distance of the propodeal seta from the propodeal spiracle shows differences, e.g., in *inexpectatus* and *nitens* (Figs 55 and 64).

11) Shape of gaster, particularly its apex, in lateral view. This is difficult to describe qualitatively but it is an important character. Soyka and Debauche both used gaster shape.

### c) Characters not yet used.

1) Body sculpture, especially of head and mesosoma. Differences occur, particularly between species of *A. (Anaphes)* and some of those placed by Huber (1992) in *Anaphes (Yungaburra)*. Whether there are consistent differences among species within either of the subgenera is not known because no one has studied surface sculpture in *Anaphes*. Cleared specimens mounted with head in face view and mesosoma in dorsal view are required to see and evaluate sculpture as a useful descriptive feature. Scanning electron microscopy should also be useful for examining sculpture, especially of the mesosoma, for differences among species.

2) Ocellar triangle shape, defined by POL, OOL, LOL. This is difficult to do since it requires a perfect dorsal view of the head (rarely found in existing slide mounts), yet it might show differences.

3) Body setae. Number and length on head and rest of body, where their position is usually constant, and perhaps on legs, the femora and tibiae particularly. This has never been studied though Soyka and Debauche suggested they had observed differences. Huber (2006) mentioned that *gerrisophaga* had strong erect setae on the mesosoma compared to other species.

4) Tarsal proportions, other than for metatarsomeres 1 and 2. No one has studied these.

5) Flagellum length in male. This likely varies quite a bit among the species. The longest flagellum is probably found in *longicornis* (hence the name) so Haliday, at least, was aware of the possible use of this character.

***Anaphes* species identification keys by authors other than Soyka.** Keys to *Anaphes* exist for at least a part of four biogeographical regions as follows.

*North America.* Girault (1911b) keyed five *Anaphes* species in section II of his key (two misplaced species of

*Erythmelus* Enock keyed out in section I). He used fore-wing proportions and shape, number of lines of microtrichia, length of fringe setae, body and appendage colour, antennal proportions and relative length of marginal space to distinguish them. Girault (1929) keyed two species of *Anaphoidea*, and six species and one subspecies of *Anaphes* in two keys. He used mainly the same features as in his previous key but sometimes in different combinations to identify species not treated previously or to synonymize others, one of them (*luna*) incorrectly. He used flagellar proportions, wing shape and colour, number lines of discal microtrichia, fineness of the microtrichia, body size and colour, to distinguish the species. Doutt (1949) keyed seven species of *Anaphoidea*, using wing shape, funicle segment proportions, ovipositor extension under mesosoma, metatarsus proportions, and body colour. In his classification of *Anaphes* species Huber (1992, 2006) keyed 9 species in the *fuscipectinis* group and 14 in the *crassicornis* group of *A. (Anaphes)*, and 6 in *A. (Yungaburra)*, using wing, antennal, and metatarsal proportions, wing colour, distribution of mps, body size, orientation of occipital groove, and length of setae between ocelli.

*South America.* Ogloblin (1962) keyed four species of *Anaphes (Austranaphes)*, using fore wing length/width and female funicle segment length/width ratios, as well as length of male parameres and propodeal structure. Huber (1992) treated the three South American species he recognized and three species from Australia in his key to *Anaphes (Yungaburra)*. He used number of claval segments, fore wing and funicle segment proportions, and presence/absence of mps and their shape to distinguish the species.

*Africa.* Huber & Prinsloo (1990) keyed the three *Anaphes (Yungaburra)* species introduced from Australia into Africa. They used wing shape and length/width ratio, and presence and shape of mps on female funicle segments to separate them. Huber & Triapitsyn (2017) described a new species, unique among *Anaphes* species in that it has a 5-segmented funicle.

*Europe.* Debauche (1948) and Hellén (1974) keyed the *Anaphes* of Belgium and Finland, respectively. Debauche keyed nine species in *A. (Anaphes)* and nine in *A. (Patasson)*. Hellén keyed eight species but did not use subgenera; the first four species keyed belong to *A. (Anaphes)* [clava 1-segmented], though his key construction suggests otherwise. Both Debauche and Hellén, who essentially followed Debauche in his species concepts and key features, used fore wing shape and proportions, antennal proportions and distribution of mps, extension of ovipositor, the number of rows of microtrichia and their qualitative features (fine or coarse), body size, leg colour and proportions of metatarsal segments, and length and density of antennal setae. In both cases, but particularly Hellén's, their application of names to species described by earlier authors is mostly incorrect. Viggiani (1994) keyed the males of 15 nominal species or species near those. His identifications were based on reared specimens, with *Anaphes* females associated with males, so he could more or less name the males to species. The obvious disadvantage is that his key treats males only, which are unknown or not definitely associated with corresponding females for most nominal species of *Anaphes*.

All of the keys listed above may fail to work for the nominal species keyed. Indeed, with few exceptions one cannot be confident that a specimen being keyed will be correctly identifiable. While this may be an overly harsh criticism of all previous keys we believe it accurately reflects the difficulty in describing features well enough to characterize and identify *Anaphes* specimens to species, assuming of course that the choice of features, either individually or in combination, used in a particular key really do distinguish a particular species from all others.

The *Anaphes* key given below is similar to those published previously in that we use the same suite of characters (not having found any new ones) and therefore almost certainly our keys suffer from the same drawbacks. However, we may have used different combinations of features than previous workers did and hope that this will make the keys work better to identify specimens correctly to species. We distinguish the more distinctive species in earlier couplets using what appear to be clear-cut, qualitative characters, e.g., presence/absence of mps on certain funicle segments, but at a certain point in the keys we have no choice but to use quantitative features, and the differences among species become relative and much more subjective.

The main difference in our keys compared to most previous ones is philosophical, but based on sound objective evidence. We accept considerably more intraspecific variation than Soyka, Debauche, and probably others realized. So for Europe our keys contain only 14 species in *A. (Anaphes)* and 15 species in *A. (Patasson)*. We were more fortunate than earlier workers in that we had access to most of the primary types whereas they did not, and we could study photographs of most of them, making comparisons easier. Whether the synonymies we propose are indeed correct will eventually have to be tested by means other than morphological. We challenge future workers to study and measure carefully the numerous Soyka paratypes, whether or not validly designated, to see if

they are conspecific with his holotypes and, if so, determine the limits of variation within each species more precisely. Clearly, this cannot be done for so many species on the basis of the original material alone because only the holotype is known. The considerable number of more recently collected specimens that have accumulated in various museums should also be carefully studied. The greatest difficulty may be matching correctly these specimens to name species based on their primary types.

### **Anaphes Haliday 1833**

**Synonymy.** Given in Huber (1992); the junior synonyms may also be determined from Tables 2, 3, and 6.

**Type species.** The type species is *Anaphes fuscipennis* Haliday (ICZN 2017). Huber *et al.* (2011, 2014) had petitioned successfully to have the type species changed.

**Diagnosis.** *Both sexes.* Body almost always uniform black or dark brown, exceptionally with metasoma almost yellow; appendages usually lighter brown, often with off-white apices of femora, tibiae and tarsi except apical tarsomere (Figs 45, 56). **Head.** Face without subantennal grooves (Fig. 3); malar sulcus absent, at most indicated exteriorly by slight change in sculpture (Fig. 5), but visible internally in cleared slide mounts (Figs 34, 35, 50, 52, 53, 60); vertex without stemmaticum but with a groove from anterior margin of posterior ocellus to supraorbital trabecula (Fig. 6); occiput with occipital groove [evidently an extension onto the occiput of the supraorbital suture of the vertex, incorrectly named the occipital suture in Huber (2006, fig. 32)] usually in line with supraorbital suture and extending ventrally to about level of lower margin of occipital foramen (Fig. 4) but sometimes short and angled inwardly towards occipital foramen (Figs 33, 62). Mandible with 3 teeth, the dorsal tooth sometimes subdivided, appearing serrate, i.e. with 2 or 3 small apical teeth (Figs 7, 8) but exceptionally (*quinquearticulatus*) with 2 large ventral teeth distinctly contrasting with 3 small, dorsal teeth (Figs 24, 25); maxilla and labium as in Figs 26 and 27. **Wings.** Wings fully developed, with posterior margin straight to slightly in basal half and slightly outcurved in apical half (Figs 39, 57, 72–79) to distinctly (Fig. 31) incurved, with apex slightly asymmetrical (anterior margin usually more curved than posterior margin), and with both dorsal and ventral surfaces almost always uniformly covered with microtrichia except for two more or less distinct bare areas (the marginal and medial spaces, small in Fig. 72) separated by an oblique row of microtrichia extending from just behind apex of stigmal vein towards wing apex (Figs 39, 57); wing retinaculum with a socketed seta near apex (Fig. 39). **Mesosoma.** Anterior scutellum (Figs 29, 30, 54, 63) without setae, with campaniform sensilla separated by about 2 or 3× their own diameter from each other and well separated from transscutal articulation, with fenestra a small triangle with rounded apices (Fig. 43, faintly indicated since below surface), and with frenum entire (Figs 13, 29); propodeum with a median longitudinal groove (Figs 13, 29, 43, 46, 54, 58, 59, 63). **Metasoma.** Petiole a thin, narrow and almost vertical crescent (Figs 40, 41, 48) longitudinally divided medially (Figs 46, 47); gaster with gt<sub>1</sub> divided medially by a longitudinal groove (Figs 17, 29, 43, 46).

**Female.** **Antenna.** Clava 1- or 2-segmented, funicle 6-segmented (Fig. 37) or, in one species, 5-segmented (Fig. 28); when 6-segmented, fl<sub>1</sub> usually the shortest segment (Figs 9, 10). **Genitalia.** Ovipositor often projecting anteriorly under mesosoma, apparently enclosed in a somewhat membranous anterior extension or sac of gaster perhaps consisting mainly of gs<sub>6</sub> (Figs 15, 18, 56, 67–70).

**Male.** **Antenna.** Flagellum distinctly 11-segmented only in species placed in *Anaphes (Yungaburra)* whereas in most nominal species flagellum appearing 10-segmented because fl<sub>1</sub> minute and either with only 1 seta (Figs 11, 12, 38) or with a seta and 1 transverse mps (Fig. 61, Huber & Prinsloo 1990, figs 13, 14). **Genitalia.** Parameres thin, each almost as long as aedeagus and with a long seta more or less midway along paramere length (Figs 22, 23, 47, 49, 59, 71).

**Variation.** A teratological specimen (UCRC) from Greece with 4 funicle segments on one antenna and 5 on the other is known. Both antennae have fl<sub>1</sub> + fl<sub>2</sub> almost completely fused and one antenna also has fl<sub>4</sub> + fl<sub>5</sub> almost completely fused (Fig. 103). All the tarsi are clearly 3-segmented (Fig. 102). Otherwise the wings (Fig. 104) and body are normal for an *Anaphes* specimen.

**Subgeneric concepts.** As mentioned above, Debauche (1948) proposed two subgenera, *A. (Anaphes)* and *A. (Patasson)*, for females with a 1- or 2-segmented clava, respectively, and provided a discussion on how they differ in other, more subtle ways. Ogleblin (1962) proposed *A. (Austranaphes)* for species from Argentina with a 2-segmented clava and males with a clearly 11-segmented flagellum. Huber (1992) treated both Debauche subgenera

as species groups within *Anaphes sensu stricto* and also proposed two subgenera, *A. (Anaphes)*, and *A. (Yungaburra)* for most of the southern hemisphere species, with Ogleblin's *A. (Austranaphes)* treated as one species group in *A. (Yungaburra)*. A major problem with Huber's classification is that the number of flagellomeres bearing mps in the male antenna must be known to classify a species into one or other subgenus. Males are so rarely associated with females that it is better to return to Debauche's subgeneric classification and reclassify the morphologically diverse species that Huber classified in *A. (Yungaburra)* into one or other of Debauche's subgenera. This, incidentally, would also be preferable for biological control workers, where *Patasson*, either as a genus or a subgenus, was used extensively prior to Huber (1992). *Patasson* should only be used as a subgenus of *Anaphes*, not a genus.

Alternatively, one could eliminate subgenera entirely and retain only species groups within *Anaphes*, reclassifying all the species previously placed in *A. (Yungaburra)* into them. If classified within the *fusciplennis* species group, for example, the species previously placed in *A. (Yungaburra)* could perhaps be distinguished from other species in the group using features such as size of the marginal and medial spaces (often considerably reduced, e.g., in *nitens*), mps shape in females (often curved apically, e.g., in *nitens*) and sculpture of the head and mesosoma (often with isodiametric reticulations, as in *quinquearticulatus*).

Finally, one could propose an entirely new species group classification but the problem would be to delimit them properly so they are easily identifiable. Huber's subgenera cannot be distinguished based on the number of claval segments in females. Some undescribed *Anaphes* from Australia and one from Indonesia, as well as *saintpierrei*, have a 1-segmented clava in contrast to other, undescribed Australian region species and *nitens*, which have a 2-segmented clava. The former would key to the *amplipennis* group of *Anaphes (Yungaburra)* which includes the South American species only (Huber 1992) and *nitens* obviously would key to his *nitens* group of *A. (Yungaburra)*, in which he included only the Australian-region species. We emphasize again that the subgeneric classification of *Anaphes* proposed by Huber (1992) is therefore rejected in favour of a return to that of Debauche (1948), i.e., with the subgenera *A. (Anaphes)* and *A. (Patasson)*. The species classified previously in *A. (Yungaburra)*, are reclassified as follows: *amplipennis*, *fijiensis*, *nunezi* and *pucarobius* into *A. (Anaphes)*, and *galtoni*, *inexpectatus*, *nitens*, and *tasmaniae* into *A. (Patasson)* (Tables 3 and 6).

## Key to European species of *Anaphes*. Females

**Note.** Within *Anaphes (Anaphes)*, the species in couplets 11–14 are difficult to distinguish unequivocally. The features used to distinguish *flavipes*, *medius*, *regulus*, and *stygius* are weak and the synonymies proposed under each are not completely certain. There may be complexes of species within each of the three species or, alternatively, the synonyms proposed are indeed synonyms but under the wrong senior synonym. The authors are not in complete agreement with each other on which synonyms should be under which species and even whether *stygius* should be treated as separate from under *regulus* or not. Finally, we may even not have synonymized enough names under one or other of the species we consider valid. Synonyms are listed alphabetically in brackets. Characters such as presence or absence of cross striations on the inner (medial) surface of the scape and relative length of the clava compared to, in particular,  $fl_5 + fl_6$  may be useful features to separate some species but need further investigation, even though Soyka used them considerably in his descriptions and keys. Only one *Anaphes (Anaphes)* species, *nipponicus*, has been described from the eastern Palearctic region. It would key to *flavipes*. See Samkova et al. (2017) for morphological features to distinguish *flavipes* from *nipponicus*.

Within *Anaphes (Patasson)*, the last two species keyed, *luna* and *silesicus*, are very similar and difficult to distinguish from one another. We may have placed some synonyms under the wrong senior synonym. Alternatively, we may have overestimated the amount of infraspecific variation and therefore placed too many species in synonymy. No *Anaphes (Patasson)* species are described from the Palearctic region east of the Ural mountains. The key could be tried for that area but may not result in correct identifications. *Anaphes inexpectatus* and *A. nitens*, introduced from Australia to control *Gonipterus* spp. on *Eucalyptus*, are established in parts of southern Europe so are included in the key.

1	Clava 1-segmented (entire) [ <i>Anaphes (Anaphes)</i> ] . . . . .	2
-	Clava 2-segmented (divided) [ <i>Anaphes (Patasson)</i> ] . . . . .	15
2(1)	$Fl_2$ and $fl_3$ without mps; fore wing with posterior margin slightly outcurved (convex) or straight . . . . .	3

-	Fl <sub>2</sub> and fl <sub>3</sub> with mps on one or both segments; fore wing with posterior margin slightly incurved (concave) . . . . .	4
3(2)	Fl <sub>4</sub> without mps [fl <sub>5</sub> and fl <sub>6</sub> the widest segments]; ovipositor extending forward under mesosoma at most to about level of base of mesocoxa; marginal space about as long as parastigma + stigmal vein. . . . .	
	[= <i>capitulatus</i> , <i>filicornis</i> , <i>maculatus</i> , <i>pratensis</i> , <i>neopratensis</i> , <i>stammeri</i> ]	
-	Fl <sub>4</sub> with at least one mps; ovipositor extending forward under mesosoma to level of head; marginal space about as long as parastigma + stigmal vein . . . . .	
	<i>A. wolfsthalii</i> (Soyka) (Fig. 87)	
4(2)	Funicle with each segment shorter than pedicel length and each not more than 2.0× as long as wide . . . . .	5
-	Funicle with at least one segment longer than pedicel and distinctly more than 2.0× as long as wide . . . . .	7
5(4)	Fl <sub>2</sub> with 2 mps; clava 1.6× as long as fl <sub>5</sub> + fl <sub>6</sub> . . . . .	
-	Fl <sub>2</sub> without mps; clava at most 1.5× as long as fl <sub>5</sub> + fl <sub>6</sub> . . . . .	6
6(5)	Fl <sub>4</sub> with 2 mps; clava same length as fl <sub>5</sub> + fl <sub>6</sub> . . . . .	
-	Fl <sub>4</sub> without mps; clava 1.5× as long as fl <sub>5</sub> + fl <sub>6</sub> . . . . .	
7(4)	Fl <sub>4</sub> without mps or (in <i>ovipositor</i> ) with 1 mps on one or both antenna . . . . .	8
-	Fl <sub>4</sub> with 2 mps . . . . .	9
8(7)	Fore wing 9× as long as wide, with longest marginal setae about 1.8× as long as widest wing width; microtrichia long, the apex of any one of them extending just past base of next one; metatarsomere 1 slightly longer than metatarsomere 2 . . . . .	
-	<i>A. ensipennis</i> (Soyka) (Fig. 76)	
-	Fore wing at most about 6.2× as long as wide, with longest marginal setae about 1.4× as long as widest wing width; microtrichia shorter, the apex of any one of them at most barely extending to base of next one; metatarsomere 1 slightly shorter than metatarsomere 2 . . . . .	
	<i>A. ovipositor</i> Soyka (Fig. 83)	
	[= <i>brevitarsis</i> , <i>germaniacus</i> (i.e., <i>angustipennis</i> Soyka not Debauche), <i>tenuipennis</i> ]	
9(7)	Metatarsomere 1 distinctly longer than 2 . . . . .	
	<i>A. crassipennis</i> (Soyka) (Fig. 75)	
	[= <i>acutipennis</i> , <i>aries</i> , <i>cultripennis</i> , <i>dilatatus</i> , <i>fennicus</i> , <i>ferrirei</i> , <i>gracillimus</i> , <i>laticornis</i> , <i>luteicornis</i> , <i>neoserenus</i> , <i>pilosipennis</i> , <i>serenus</i> , <i>siegerfeldi</i> , <i>sulphuripes</i> , <i>tarsalis</i> , <i>thoracicus</i> , <i>wertaneki</i> ]	
-	Metatarsomere 1 at most slightly longer than metatarsomere 2, but usually equal or slightly shorter than 2 . . . . .	10
10(9)	Fl <sub>2</sub> at most 2.4× as long as wide; fl <sub>1</sub> + fl <sub>2</sub> together not longer than fl <sub>3</sub> . . . . .	
	[= <i>avalae</i> , <i>breviventris</i> , <i>flavus</i> , <i>leonhardwitzii</i> , <i>nigricornis</i> ]	
-	Fl <sub>2</sub> at least 2.5× as long as wide; fl <sub>1</sub> + fl <sub>2</sub> together longer than fl <sub>3</sub> . . . . .	11
11(10)	Fore wing at most 4.4× as long as wide, with marginal setae less than 0.8× maximum wing width; marginal space separated from medial space by double line of microtrichia; hind wing fairly wide, apparently with two irregular rows of several microtrichia . . . . .	
-	<i>A. arenbergi</i> Debauche (Fig. 73)	
-	Fore wing at least 4.7× as long as wide, with marginal setae at least 0.9× maximum wing width; marginal space separated from medial space by a single line of microtrichia; hind wing narrower, with at most one irregular line of a few microtrichia . . . . .	12
12(11)	Clava at most 3.2× as long as wide . . . . .	13
-	Clava at least 3.4× as long as wide . . . . .	14
13(12)	Ovipositor sheaths at least about 1.1× as long as metatibia . . . . .	
	[= <i>intermedius</i> , <i>lacensis</i> , <i>pulchripennis</i> , <i>ranalteri</i> , <i>speciosus</i> ]	
-	Ovipositor sheaths at most about 1.0× as long as metatibia . . . . .	
	[= <i>autumnalis</i> , <i>gracilior</i> , <i>soykai</i> (i.e., <i>crassicornis</i> Soyka not Walker)]	
14(12)	Fore wing with apex narrower and slightly more pointed; clava at least 3.9× as long as wide . . . . .	
	<i>A. flavipes</i> Förster (Fig. 77)	
	[= <i>antoniae</i> , <i>auripes</i> , <i>ciliatus</i> , <i>elegans</i> , <i>lemae</i> , <i>longispinosus</i> , <i>mirabilis</i> , <i>neospecialis</i> , <i>pilicornis</i> , <i>piliscapus</i> , <i>spinosus</i> , <i>varicolor</i> ]	
-	Fore wing with apex wider and slightly more rounded; clava at most 3.8× as long as wide . . . . .	
15(1)	<i>A. stygius</i> Debauche (Fig. 86)	
	Back of head with occipital groove short, directed medially towards occipital foramen, thus forming an angle with supraorbital trabecula and strongly diverging away from posterior margin of eye (Fig. 33); fore wing posterior margin with either a short hyaline section subapically, separating distal dark margin from proximal dark margin or entire posterior margin hyaline, contrasting with dark anterior margin . . . . .	16
-	Back of head with occipital groove longer, not directed medially towards occipital foramen, thus in line with supraorbital trabecula and weakly diverging from posterior margin of eye (Figs 4, 90c); fore wing posterior margin almost always without a short hyaline section subapically (e.g. Figs 31, 39, 94), the entire posterior and apical margin uniformly dark . . . . .	19
16(15)	Marginal and medial spaces small, and medial space delimited posterobasally by at least 3 lines of microtrichia; fl <sub>2</sub> –fl <sub>6</sub> with J-shaped mps (fig. 7 in Huber & Prinsloo 1990; Fig. 60); fore wing wide, with apex distinctly truncate (fig. 1 in Huber & Prinsloo 1990; Fig. 72) . . . . .	
	<i>A. nitens</i> (Girault) (Figs 60–72)	
	[= <i>gonipteri</i> ]	
-	Marginal and medial spaces larger and more distinct, and medial space delimited posterobasally by 1 line of microtrichia; fl <sub>5</sub> –fl <sub>6</sub> with straight mps (e.g., fig. 9 in Huber & Prinsloo 1990, and figs 43 and 46 in Huber 1992); fore wing narrower, with apex more evenly rounded (e.g., fig. 3 in Huber & Prinsloo 1990, and figs 27 and 28 in Huber 1992) . . . . .	17
17(16)	Ovipositor extending forward almost to head, trombone shaped; fl <sub>4</sub> without mps (occasionally with 1 mps), the segment shorter and narrower than fl <sub>3</sub> or fl <sub>5</sub> . . . . .	
	<i>A. collinus</i> Walker (Fig. 90)	
	[= <i>aestivus</i> , <i>aterrimus</i> , <i>declinatus</i> , <i>discolor</i> , <i>discolorsimilis</i> , <i>latus</i> , <i>minor</i> , <i>nigerrimus</i> , <i>ornatus</i> , <i>ovatus</i> , <i>pallidus</i> , <i>pal-</i>	

	<i>lipes, relictus, stubaiensis, tenuis, trijohanni]</i>
-	Ovipositor extending forward at most to level of mesocoxa; fl <sub>4</sub> with 2 mps (occasionally with 1 mps in <i>inexpectatus</i> or no mps in <i>brevis</i> , the segment usually as long and wide as fl <sub>3</sub> or fl <sub>5</sub> , but sometimes shorter (Figs 36, 37) . . . . . 18
18(17)	Funicle segments longer, length/width of fl <sub>2</sub> –fl <sub>5</sub> each at least 3.1 . . . . . <i>A. brevis</i> Walker (Figs 32–49) [= <i>brunneus</i> , <i>latipterus</i> , <i>maculicornis</i> , <i>malchinensis</i> , <i>maradonae</i> , <i>pectoralis</i> , <i>pinguicornis</i> , <i>rotundipennis</i> ]
-	Funicle segments shorter, Length/width of fl <sub>2</sub> –fl <sub>5</sub> each at most 2.9 . . . . . <i>A. inexpectatus</i> Huber & Prinsloo (Figs 50–59)
19(15)	Fl <sub>2</sub> –fl <sub>4</sub> without mps; fore wing narrow and parallel sided, its width near apex equal to width at apex of venation. . . . . ..... <i>A. angustipennis</i> Debauche (Fig. 88)
-	Fl <sub>2</sub> –fl <sub>4</sub> with 1 or 2 mps on at least one of the segments, usually on two or three of them . . . . . 20
20(19)	Fl <sub>2</sub> with 1 or 2 mps . . . . . 21
-	Fl <sub>2</sub> without mps . . . . . 24
21(20)	Fl <sub>2</sub> with 1 mps . . . . . [ <i>superadditus</i> ] Fl <sub>2</sub> with 2 mps . . . . . 22
22(21)	Fl <sub>6</sub> at most 2.2× as long as wide . . . . . <i>A. maialis</i> Debauche (Fig. 99) [= <i>aequus</i> , <i>devius</i> , <i>semiflavus</i> , <i>vulgarisimilis</i> ] Fl <sub>6</sub> at least 3.0× as long as wide . . . . . 23
23(22)	Fore wing narrow, at least 6.0× as long as wide; ovipositor shorter than gaster, at most 0.8× as long as metatibia, not extending under mesosoma; metatarsomere 1 distinctly longer than metatarsomere 2 [scape narrow, with ventral margin not very convex; fore wing with marginal space long] . . . . . <i>A. lineipennis</i> (Soyka) (Fig. 95) [= <i>chrysomelae</i> , <i>dessarti</i> , <i>longipennis</i> , <i>obscurus</i> , <i>semimedium</i> ] Fore wing wider, at most 5.6× as long as wide; metatarsomere 1 at most only slightly longer than metatarsomere 2; ovipositor at least as long as gaster, at least 1.1× as long as metatibia . . . . . <i>A. longicornis</i> Walker (part) (Figs 96, 97 [male]) [= <i>acutiventris</i> , <i>additus</i> , <i>archettii</i> , <i>ater</i> , <i>balteatus</i> , <i>campestris</i> , <i>communis</i> , <i>consimilis</i> , <i>distinctus</i> , <i>dubius</i> , <i>duplicatus</i> , <i>elongatus</i> , <i>eu-longicornis</i> , <i>fabarius</i> , <i>falsus</i> , <i>flavitarsis</i> , <i>kressbachi</i> , <i>leptoceras</i> , <i>longior</i> , <i>malkwitzi</i> , <i>neodistinctus</i> , <i>neoflavus</i> , <i>pallidicornis</i> , <i>pannonicus</i> , <i>piceicornis</i> , <i>rufus</i> , <i>timidus</i> ]
24(20)	Ovipositor not extending forward under mesosoma, shorter than almost globular and apically rounded gaster and less than 0.7× as long as metatibia; fl <sub>2</sub> shorter than pedicel and shorter than fl <sub>3</sub> , at most 1.7× as long as fl <sub>1</sub> . . . . . ..... <i>A. diana</i> (Girault) (Fig. 94) [= <i>apilosus</i> , <i>compressus</i> , <i>globosus</i> , <i>heterotomus</i> , <i>lameerei</i> , <i>minimus</i> , <i>niger</i> , <i>parciventris</i> , <i>reductus</i> , <i>valkenburgicus</i> ] Ovipositor extending at least slightly forward under mesosoma and at least 1.1× as long as metatibia; fl <sub>2</sub> almost always at least as long as pedicel, at least as long as fl <sub>3</sub> and at least 2.0× as long as fl <sub>1</sub> . . . . . 25
25(24)	Metatarsomere 1 distinctly longer than metatarsomere 2 . . . . . 26
-	Metatarsomere 1 shorter, equal to or, at most, barely longer than metatarsomere 2 . . . . . 27
26(25)	Fore wing at least 8.0× as long as wide . . . . . <i>A. parallelipennis</i> (Soyka) (Fig. 100) [= <i>rectipennis</i> ] Fore wing at most 6.0× as long as wide . . . . . <i>A. longicornis</i> Walker (part) [ <i>gabitzi</i> , <i>medioacutus</i> , <i>sibbei</i> ]
27(25)	Ovipositor at least 1.7× as long as metatibia length . . . . . <i>A. crassus</i> (Soyka) (Fig. 89) [= <i>stratipennis</i> ] Ovipositor at most 1.6× as long as metatibia length . . . . . 28
28(27)	Fore wing at least 9.0× as long as wide . . . . . <i>A. crassipilis</i> (Soyka) (Fig. 92) [ <i>linearis</i> ] Fore wing at most 7.6× as long as wide . . . . . 29
29(28)	Fore wing with microtrichia on dorsal surface of membrane long, the apex of microtrichia usually overlapping the base of the next . . . . . <i>A. crassicornis</i> (Walker) (Fig. 91) [ <i>arcuatus</i> , <i>fortipennis</i> , <i>longipilis</i> , <i>nemorosus</i> , <i>lucidus</i> , <i>serbiculus</i> , <i>variatus</i> , <i>weidenhofi</i> ] Fore wing with microtrichia on dorsal surface of membrane shorter, the apex of each not usually extending to base of the next . . . . . 30
30(29)	Metatarsomere 1 as long as metatarsomere 2; fl <sub>2</sub> usually as long as fl <sub>3</sub> . . . . . <i>A. luna</i> (Girault) (Fig. 98) [ <i>aequipennatus</i> , <i>albipes</i> , <i>bicolor</i> , <i>brachygaster</i> , <i>devillei</i> , <i>differens</i> , <i>dorcas</i> , <i>euryle</i> , <i>hundsheimensis</i> , <i>neobrevior</i> , <i>neustadtii</i> , <i>ordinarius</i> , <i>palliditarsis</i> , <i>pilosissimus</i> , <i>speciosior</i> , <i>swiedecki</i> , <i>vulgaris</i> , <i>wratislawensis</i> ] Metatarsomere 1 shorter than metatarsomere 2; fl <sub>2</sub> usually shorter than fl <sub>3</sub> . . . . . <i>A. silesicus</i> (Soyka) (Fig. 101) [ <i>brevior</i> , <i>calvescens</i> , <i>exiguus</i> , <i>exiguosimilis</i> , <i>flavicornis</i> , <i>neobrevior</i> , <i>obsoletus</i> , <i>pellucens</i> , <i>similis</i> ]

## Hosts and biology

Huber (1986) listed genera or species in 19 insect families as hosts of *Anaphes* species based on the published literature but several of them (Cecidomyiidae, Cicadellidae, Delphacidae, Diaspididae, Gelechiidae, Gracillariidae, Membracidae, Tingidae) are likely incorrect. Host records from literature published since 1985 and unpublished

host records from *Anaphes* specimens seen in collections are listed in Table 7. The published records are mostly summarized from Noyes (2016), who included about 140 host records (including those prior to 1985) and several acknowledged errors. Further rearings will validate previous host records and, we hope, add new host records if care is taken to confirm the host/parasitoid association by isolating identified host eggs individually in gelatin capsules to rear out any parasitoids present within. From the published literature it is clear that *Anaphes* species are mainly egg parasitoids of Chrysomelidae and Curculionidae (Table 7). In some cases, e.g., *Neocoenorrhinus pauxillus* (Germar) (Curculionidae), the *Anaphes* specimens were reared on separate occasions by different people from widely separated localities (England, Russia) so the association are almost certainly correct. But for others there may be only one published host record. Confirmation of any of the records is thus desirable.

**TABLE 7.** Hosts of *Anaphes* species compiled from the literature from 1985–2015 and from unpublished hosts recorded for *Anaphes* specimens in collections. Older records are included if they were missed by Huber (1986). Names of beetle hosts from Europe are updated according to the latest catalogues of Palearctic Coleoptera (the names as cited in the references below or on specimens may have different generic combinations or are synonyms of older names). Some slide labels may indicate “with egg of” so it is not certain that the *Anaphes* was actually reared from that host. Additional careful rearing from the hosts listed is desirable to confirm all host associations and host identities, and to obtain fresh *Anaphes* specimens for molecular study. Usually one *Anaphes* species is listed from each host although occasionally two or more morphospecies may have been reared from a named host and are listed.

Host taxon	Published reference or specimen depository	<i>Anaphes</i> nominal species as given in each reference. Identifications by present author(s) are in bold
<b>Byrrhidae</b>		
<i>Lioon simplicipes</i> (Mannerheim)	Huber (1992)	<b><i>byrrhidiphagus</i></b>
<b>Chrysomelidae</b>		
<i>Cassida rubiginosa</i> (Müller)	Cox (1994)	<i>pannonicus</i>
<i>C. algirica</i> Lucas	Cox (1994)	<i>pannonicus</i>
<i>Dicladispa testacea</i> (L.)	Viggiani (1994)	near <i>maialis</i>
<i>Lilioceris lilii</i> (Scopoli)	Kenis <i>et al.</i> (2003)	<b><i>debilipennis</i></b>
<i>L. merdigera</i> (L.)	Kenis <i>et al.</i> (2003)	<b><i>debilipennis</i></b>
<i>Chrysolina staphylaea</i> (L.)	ZMUC	<b><i>lineipennis</i></b>
<i>Longitarsus jacobaea</i> Waterhouse	BMNH	
<i>L. quadriguttatus</i> (Pontoppidan)	Thuróczy collection	? <i>crassicornis</i> Walker
<i>Sphaeroderma rubidium</i> Graells	Labeyrie (1962)	
<b>Curculionidae</b>		
<i>Apion semivittatum</i> (Gyllenhal)	Viggiani & Jesu (1988)	? <i>heterotomus</i>
<i>Auleutes epilobii</i> (Paykull)	Huber <i>et al.</i> (1997)	<i>victus</i>
<i>Baris interstitialis</i> (Say)	Huber <i>et al.</i> (1997)	? <i>sordidatus</i>
<i>Brachypera crinitus</i> (Boheman)	Baccetti (1958)	<i>luna</i>
<i>Ceratapion basicorne</i> (Illiger)	Clement <i>et al.</i> (1989)	
<i>Ceutorhynchus cruciger</i> (Herbst)	Thuróczy collection	
<i>C. trimaculatus</i> Fabricius	CNC	
<i>Conotrachelus anaglypticus</i> (Say)	Huber <i>et al.</i> (1997)	<b><i>conotracheli</i></b>
<i>C. schoofi</i> Papp	Tedders & Payne (1986)	? <i>conotracheli</i>
<i>Cosmopolites sordidus</i> Germar	Huber <i>et al.</i> (1997)	<i>victus</i> (laboratory test)
<i>Curculio</i> sp. [Jesu, pers. comm.]	Jesu (2001)	<i>trijohanni</i> ( <i>collinus</i> )
<i>Hypera rumicis</i> (L.)	Thuróczy collection	
<i>Hypera zoilus</i> Scopoli	Baccetti (1957)	<i>luna</i>
<i>Isochnus sequensi</i> Stierlin	Thuróczy collection	
[named as <i>Rhynchaenus populi</i> on slides]		
<i>Liophloeus tessulatus</i> (O.F. Müller)	Thuróczy collection	<i>longicornis</i>
<i>Listronotus oregonensis</i> (Le Conte)	Huber <i>et al.</i> (1997)	<i>listronoti, victus, cotei</i>
<i>L. sparsus</i> (Say)	Huber <i>et al.</i> (1997)	<i>listronoti, victus</i>
<i>L. texanus</i> (Stockton)	Boivin <i>et al.</i> (1990)	

.....continued on the next page

TABLE 7. (Continued)

Host taxon	Published reference or specimen depository	<i>Anaphes</i> nominal species as given in each reference. Identifications by present author(s) are in bold
<i>Lixus junci</i> Boheman	Viggiani (1994)	<i>longicornis</i>
<i>Lixus</i> sp.	Thuróczy collection	<i>pectoralis</i>
<i>Microlarinus lareynierei</i> (Duval)	Viggiani (1994)	<i>maialis</i>
<i>Nedyus flavicaudis</i> (Boheman)	Huber <i>et al.</i> (1997)	<i>victus</i>
<i>Neochetina eichhorniae</i> Warner	Huber <i>et al.</i> (1997)	<i>victus</i> (laboratory test)
<i>Neocoenorhinus pauxillus</i> (Germar)	Blommers & Vaal (2002)	<i>brachygaster</i>
<i>Orcheses fagi</i> (L.)	Thuróczy collection	<i>collinus</i>
<i>O. quercus</i> (L.)	Viggiani (1994)	near <i>stygius</i>
<i>Oryxolaemus crocei-femoratum</i> (Gyllenhal)	Viggiani & Jesu (1988)	
<i>Phrydiuchus topiarius</i> (Germar)	Andres & Rizza (1965)	
<i>Phytobius</i> sp.	BMNH	
<i>Rhabdoscelis obscurus</i> (Boisduval)	Beardsley (2000)	<i>calendrae</i>
<i>Rhinocyllus conicus</i> (Froehlich)	Woodburn (1996)	
<i>Sciaphobus squalidus</i>	Gyllenhal	Thompson (1958)
<i>Sitona bicolor</i> Fåhraeus	Aeschlimann (1986)	<i>diana</i>
<i>S. concavirostris</i> Hochhuth	Aeschlimann (1986)	<i>diana</i>
<i>S. callosa</i> Gyllenhal	Aeschlimann (1986)	<i>diana</i>
<i>S. flavescentis</i> (Marsham)	Huber (2006)	<i>diana</i> (laboratory test)
<i>S. humeralis</i> Stephens	Aeschlimann (1986)	<i>diana</i>
<i>S. sulcifrons deubeli</i> Gyllenhal	Aeschlimann (1986)	<i>diana</i>
<i>S. tenuis</i> Rosenhauer	Aeschlimann (1986)	<i>diana</i>
<i>Sphenopterus cariosus</i> (Olivier)	Beardsley (2000)	<i>calendrae</i>
<i>S. venatus vestitus</i> Chittenden	Beardsley (2000)	<i>calendrae</i>
<i>Stenocarus ruficornis</i> (Stephens) (as <i>fuliginosus</i> Marsham)	Viggiani (1994)	cf. <i>calvescens</i>
<i>Trichobaris bridwelli</i> Barber	Cuda & Burke (1991)	
<b>Ephydriidae</b>		
<i>Parydra aquila</i> (Fallén)	Meyers & Deonier (1992)	
<b>Kateretidae</b>		
<i>Brachypterus glaber</i> (Newman)	BMNH	
<b>Lestidae</b>		
<i>Lestes</i> sp.	Huber (2006)	
<b>Miridae</b>		
<i>Lygocoris pabulinus</i> (L.)	?collection	
<i>Lygus pratensis</i> (L.)	Viggiani (1994)	near <i>calvescens</i>
<i>L. rugulipennis</i> Poppius	BMNH	<i>medius</i> (misidentified as <i>fuscipennis</i> in Varis 1972)
<i>Lygus shulli</i> Knight	McGregor <i>et al.</i> (2000)	<i>iole</i>
<b>Tenthredinidae</b>		
<i>Ametastegia glabrata</i> (Fallén)	BMNH	
<i>Macrophya punctumalbum</i> (L.)	Thuróczy collection	<i>crassipenis</i>
<i>Pontania</i> sp. (in gall)	Thuróczy collection	
<b>Tipulidae</b>		
<i>Tipula paludosa</i> Meigen	Kelly (1990)	

Because *Anaphes* contains species important in natural and biological control any productive work on them for potential use in the latter requires that they be identified with confidence. This cannot be done at present for most European species and few species from elsewhere as well, so the *Anaphes* species we list will have to be checked again with longer series of freshly reared material from any of the previously listed hosts identified to species or from other hosts whose eggs have not yet been reared. Before proper preparation for morphological study, DNA/RNA should be extracted and suitably preserved from the reared specimens of *Anaphes* and their hosts, if possible.

Two contrasting situations have been found for a given *Anaphes* species reared from known hosts that were correctly identified to species (host identification is almost impossible based on eggs only—the host has to be reared or its eggs and adults correctly associated in some other way): 1) two or more *Anaphes* species were reared from a single host species, and 2) a single *Anaphes* species was reared from two or more hosts in the same host species or genus, different host genera in the same family, or different families in the same or different insect orders. Several examples are given.

1) In North America, *listronoti* and *victus* were reared from *Listronotus oregonensis* LeConte (Curculionidae) in Quebec and *cotei* was reared from *L. oregonensis* in Nova Scotia (Huber *et al.* 1997). Biological differences such as whether the species were solitary or gregarious, their gait (the way they walked), and morphological differences showed that three *Anaphes* species were present. This was confirmed for two of the species (from Quebec rearings) with cross-breeding experiments, though depending on the cross some interbreeding occurred.

2) In Europe, two (possibly three) different *Anaphes* species were reared from *Sitona humeralis* Stephens and other *Sitona* spp. (Curculionidae) (Aeschlimann 1975). One species, *diana*, was by far the most common. Another, apparently different and unidentified, species was also reared.

3) In North America, *iole* has been reared from several *Lygus* spp. (Miridae) (Jackson & Graham 1983; McGregor *et al.* 2000) and *behmani* has been reared from several *Hypera* spp. (Curculionidae) (Puttler *et al.* 1973).

In the above cases, hosts in the same family were parasitized by one or more of the *Anaphes* species. In contrast, the best example of an *Anaphes* species reared from two different insect orders in North America is *conotracheli*, from *Conotrachelus nenuphar* (Herbst) (Coleoptera: Curculionidae) and *Ragoletis pomonella* (Walsh) (Diptera: Tephritidae) (Huber 2006).

Where host range has been studied for one *Anaphes* species whose females parasitize several host species in the same genus it was shown experimentally that the females would parasitize all of them, e.g., *Lygus* spp. (Jackson & Graham 1983), *Sitona* (Aeschlimann 1986), *Sphenopterus* spp. [as *Calendra* spp.] (Satterthwaite 1931). When two different host genera, *Lygus* spp. and *Pseudotomoscelis seriatus* (Reuter), were tested in the same family, Miridae, e.g., for *iole* the *Anaphes* progeny parasitized specimens in both host genera but showed considerable, non-overlapping morphological differences (Huber & Rajakulendran 1988). When the host families were different, e.g., *iole* on *Lygus* (Miridae) and *Nabis* spp. (Nabidae) hosts very few parasitoid adults emerged successfully from *Nabis* compared to *Lygus* (Jackson & Graham 1983).

Whereas *Anaphes* females of at least some species may have definite host preferences, others appear to be opportunistic as shown by laboratory experiments and the use of factitious hosts to maintain colonies. Traoré (1995) maintained a lab colony in Benin of two biotypes of the North American *victus* on the factitious host *Neochetina eichhorniae* Warner (Curculionidae), with 70–90% successful emergence. He used specimens confined in Petri dish experiments to see if the banana weevil, *Cosmopolites sordidus* Germar (Curculionidae), would also be parasitized. This major banana pest originated from Asia but is present in Africa and elsewhere. Both biotypes of *victus* did indeed parasitize successfully the ‘new’ host eggs, which are larger than those of their normal host *L. oregonensis*, but few first generation adults managed to emerge, apparently for two reasons. First, the developing larvae could not consume all the egg contents and the uneaten portion of the vitellus then decayed and became lethal to the adult parasitoid before it could emerge. Second, the chorion of *C. sordidus* is too thick for most surviving *victus* adults to chew their way out. Thus, on average only about 2% of the 57% of *victus* that completed development managed to emerge successfully from the *C. sordidus* eggs. In another case, the North American *calendrae* was successfully reared on *Rhabdoscelis obscurus* (Boisduval), a weevil pest of sugarcane (Bianchi 1964) on at least one occasion in a laboratory in the Hawaiian Islands but was never found on this weevil in the field (Beardsley 2000). More such experiments on host preference among a variety of hosts of the same species, genus, or family offered simultaneously or sequentially to females of a given *Anaphes* species are needed to evaluate the host preferences of yet other species of the genus.

Why are *Anaphes*, and other Mymaridae, apparently so opportunistic and capable of developing on more than one species of host? The most likely reason is that females evidently oviposit mainly (or only?) in freshly laid host eggs whose larvae have not yet developed to the point of having an immune system. Insect eggs may have an immune response to insect parasitization, as shown for *Trichogramma* in one species of moth (Abdel-latief & Hilker 2008) but, despite this example, host eggs are essentially defenceless against insect parasitism and they only may avoid being parasitized by being laid in concealed places such as plant tissue or among soil particles where they may better escape detection. Insect eggs, those nicely packaged, defenceless little containers of nutrients, need

only to be found and parasitized, and any mymarid larva inside probably has a good chance of developing successfully to adulthood, almost regardless of the host insect taxon. However, the two examples given above show that this is not always the case. Both are examples of physical, not chemical/physiological protection by the host. Chorion thickness (the banana weevil example) and perhaps a covering of viscous material on the eggs of some species, e.g., Colorado potato beetle, *Leptinotarsa decemlineata* Say (Chrysomelidae) (Couturier 1935), is the only intrinsic protection the host eggs have, though in the latter case it was clear that the female adult would apparently successfully lay her egg(s) in the host and definitely kill it but no offspring developed successfully to adulthood.

We hypothesize that any host egg of suitable size laid in an appropriate microhabitat, i.e., in which females of any given species of egg parasitoid searches, would be subject to parasitism. This may apply to any species of Mymaridae or other egg parasitoid. And, given this likely opportunism, we suggest that egg parasitoids may not be the most suitable agents for classical biological control introductions because their target host specificity may not be sufficient for safe release into a new location without potentially unintended environmental consequences on non-target insects. With respect to taxonomy of Mymaridae we further suggest that intraspecific morphological variation may be greater than currently assumed, with the result (as evidenced particularly in the present paper) that more morphospecies are described than actually exist. Molecular evidence as an independent test is greatly needed, though there is no intrinsic reason why such intraspecific variation may not also occur there too and be misinterpreted as representing a complex of closely related but biologically different species. It must be emphasized, however, that the converse is also possible and perhaps likely. Apparently identical morphospecies may indeed be good biological species, separable on behavioral or other features. For classical biological control at least, case by case studies of particular taxa must be undertaken before release.

Over 60 years have elapsed since Soyka's last *Anaphes* descriptions and 21 nominal species have been described since then (Table 2) but little biological work has been done on any of them and there are very few host records. Our attempt to synonymize names proposed by Soyka and others will, we hope, encourage more biological work on *Anaphes* (or other Mymaridae) as well as more detailed taxonomic work on particular species without the burden of so many unidentifiable nominal species to contend with. The enormous number of insect eggs (relative to other life stages) present in most habitats explains why Mymaridae are so commonly collected throughout the growing season but particularly in spring and early summer. So a good opportunity exists to discover parasitized host eggs, particularly of pest weevils or leaf beetles, for experimental work on host associations under laboratory conditions.

**TABLE 8.** Abbreviations of morphological terms as used in Figures

aed = aedeagus	lpm = lateral panel of metanotum
as = anterior scutellum	man = mandible
ax = axilla	max = maxilla
axl = axillula	mlm = median lobe of mesoscutum
axp = axillar pit	no <sub>1</sub> = pronotum
cx <sub>1</sub> = procoxa	not = notaulus
dor = dorsellum	oc = occiput
fl = funicle segment (females) or flagellomere (males)	ocf = occipital foramen
fre = frenum	par = paramere
fu <sub>2</sub> p = mesofurcal pit	pl <sub>3</sub> = metapleuron
gen = gena	ppd = propodeum
gs = gastral sternum	pre = prepectus
gt = gastral tergum	psg = postgena
hsc = hypostomal carina	ptl = petiole
lab = labium	st <sub>1</sub> = prosternum
llm = lateral lobe of mesoscutum	tmp = temple
lpa = lateral panel of axilla	tsa = transscutal articulation

## Discussion

Soyka clearly was an extreme splitter. This is evident from the number of species he described in most of the genera (often his own) he studied. The result was that the Palearctic Region (mainly the European part) had a fauna of Mymaridae exceeding 500 nominal species, well above the Australian region, the area with the next highest number (about 300) of nominal species (Huber 1986, Lin *et al.* 2007). Besides *Anaphes* the larger genera in which Soyka had described numerous species are *Alaptus* Westwood, *Anagrus* Haliday, *Camptoptera* Foerster, *Ooconus* Haliday, and *Polynema* Haliday. Many synonymies of Soyka species have already been proposed for *Alaptus* (Triapitsyn 2017), *Anagrus* (Chiappini 1989), *Camptoptera* (Triapitsyn 2014) and *Ooconus* (Triapitsyn 2010), thereby already reducing considerably the number of valid species for Europe.

The number of species Soyka described in European *Anaphes* is over twice that in the next largest genus, *Polynema*, the only remaining genus whose Soyka species (among others) need sorting out. In *Anaphes*, even the slightest change in colour, relative length of two or more antennal segments, or fore wing length/width ratios evidently indicated to Soyka that a specimen he had before him was a different species from some other specimen he had described. Soyka's typological approach, as reflected in his descriptions and identification keys for all the genera he treated, thus indicated no more than differences among individual specimens, not differences among species. Soyka (1949: 398) himself stated in a paragraph at the end of his *Fulmekiella* species key that the last six of his species were difficult to separate and he even admitted that if the measurements are not exact enough or the preparation not favorable the species should be checked for both features to distinguish them (he used more than two features in those couplets). Yet he still described them as distinct species! For example, we found that five of his *Fulmekiella* species (*ater*, *campestris*, *consimilis*, *dubius*, and *malkwitzi*) are the same as *longicornis*. The other species, *cinctus*, listed in this difficult "complex" occurs twice in that key and nowhere else. Soyka's apparent obsession to describe new species evidently made him think that with more accurate measurement or better preparation techniques one would be able to distinguish the specimens better. Whereas this is true with better specimen preparations it is not necessarily so with more accurate measurements. At the end of his "remarks on the systematics of species" section he stated "Der Werte dieser Merkmale, ihre Konstanz und Variationsbreit, wird in einer spaeteren Arbeit ausfuehrlich behandelt, da fuer viele Arten hunderte von Examplaren zur Verfuegung stehen" (the value of these characters, their consistency and variation, will be treated in detail in a later work, because for many species hundreds of exemplars stand [are] at [my] disposal). He also admitted "Da viele Artmerkmale sehr variabel sind, wurde in den Tabellen darauf besondere Ruecksicht genommen. So ist die Behaarung sehr variabel." (Because species diagnostic characters are very variable, therefore particular notice of them was taken in the Tables [keys]. Thus, the pilosity is very variable.) He never published a discussion on variability. Furthermore, as his descriptions and identification keys illustrate, and as we emphasize again, Soyka almost always treated even the slightest perceived differences as indicative of species differences rather than intraspecific variation, which he obviously could not have assessed because he described so many of his species from a single specimen only. We illustrate here an example of the problem of variation, where the left and right antenna on the **same** specimen of *brevis* has different proportions in at least one of the segments (Figs 36, 37).

Soyka (1949: 306) stated in his biology and ecology section with regard to *calendrae* Gahan (1927), that "Es wurden 123 Examplare gezuechtet in so verschiedener Groesse, das der Verfasser es nicht veruebeln moege, wenn trotz allem die Vermutung ausgesprochen wird, dass es sich doch um Verschiedene Artet handelt" (there were 123 specimens reared in such a range of size, that the researcher [Gahan] might not be blamed if the suspicion is expressed that one was, in contrast, dealing with several species). One wonders how Soyka would have described the 123 specimens had he had access to them. Soyka (1949: 307) also criticized the observation by Bakkendorf (1934: 55), who suggested that the number of hitherto described *Anaphes* and *Anaphoidea* species (he treated these as distinct genera) must be reduced, by stating flatly [English translation] that "Bakkendorf's observation is unsound and is to be rejected, and that the opposite is the case."

Soyka attempted to summarize the known hosts for *Anaphes* and concluded correctly that they mainly parasitize Coleoptera eggs but that there were too few rearings. He did not rear any *Anaphes* himself but stated that the largest numbers of his species were collected either in fields or, for the Hundsheim, Malchin and Kressbach specimens, at the window of hay stalls. Those collected from hay lofts (the Stubaital specimens, likely) also originated from [alpine] hay fields. As mentioned above, Soyka explained in detail where his window collecting was done in Valkenburg. The window(s) in question were on the uppermost floor of a student house (Studienhaus)

whose inner wall was covered with vines up to a height of 15 m; the “animals” were blown in on wind currents from surrounding fields through an open window where he caught them. Soyka thus determined that fields are the most important biotope for the *Anaphes* genus-group. Given the rather limited range of habitats from which he obtained most of his specimens Soyka could hardly come to any other conclusion. It certainly reduced even more the likelihood that his coverage of *Anaphes* species in Europe was complete. On the contrary, describing so many species from so few habitats suggests even more strongly that most of his species could not possibly be anything more than synonyms of one another or those described by earlier workers.

Soyka discussed five different geographical regions in which he collected *Anaphes* species. While the distinctions are fairly accurate regarding climate, they really only reflect the places where Soyka lived and/or collected. Using his terms for climate they are: Valkenburg with a maritime climate, Hundsheim with a partly steppic climate, Stubaital with an alpine climate, and Meklenburg with a northern plain climate. The fifth area consisted of isolated places in Schlesien or Oberschlesien (German names for Silesia and Upper Silesia), for what is today the Voivodeship of Lower Silesia, which since 1945 are in Poland and further east, the material of which Soyka claimed he did not have time to study. To what extent Soyka used these regional differences to support his species concepts is unclear but the evidence suggests that it was considerable because he did not record a single one of his *Anaphes* species from more than one locality. He was apparently also unaware of any species described by other authors with distributions consisting of more than a single locality. But even if he was aware, the presence of appropriate hosts is much more important in determining the range of a given *Anaphes* species, which often have wide distributions. For example, *diana* occurs in southern Europe from southwestern Spain to Greece (Aeschlimann 1977) and east to Syria and eastern Turkey (Aeschlimann 1986) while in northern Europe it occurs in England eastwards possibly to Russia, though the identity of the Russian specimens is uncertain. In contrast, Aeschlimann (1975) did not find *diana* in Algeria, Morocco and Tunisia. Another species in the Palearctic Region, *fuscipennis*, has a wide north-south distribution from Sweden to Algeria and Tunisia and east-west distribution from Spain to Hungary (specimens in CNC). In the Nearctic Region, *fuscipennis* was first introduced, apparently by accident, into Utah, USA, in 1911 and now occurs from Newfoundland to British Columbia in Canada and south to Florida in the USA. Huber (1992) showed, however, that at least two independent introductions must have occurred. The species evidently spread widely from those points. Interestingly, *flavipes* is widespread in Europe and established in eastern USA but failed to establish in inland northwestern USA, where the humidity is low (Roberts 2016). Relative humidity may thus be an important climatic factor in determining geographical distribution of some *Anaphes* species.

Debauche (1948) was the second most prolific describer of European *Anaphes* so comments on his work are necessary. He described 14 species from 63 female and 17 male primary and secondary types, 28 of which were for 1 species, *lameerei*. His descriptions were published between Soyka’s earlier and later *Anaphes* papers though he had actually finished his manuscript on Christmas day, 1943 (Debauche 1948: 239), 2.5 years before Soyka’s first *Anaphes* publication. The five-year delay in Debauche’s publication was likely due to the war in Europe. The result is that 11 of Soyka’s *Anaphes* species have priority over the 14 Debauche species. Debauche’s work was almost unknown to Soyka (less so *vice versa*). This is not surprising because their papers containing *Anaphes* descriptions appeared within a period of 11 years, and only a year separated the two largest ones. Post war politics and the fact that Debauche published in French and Soyka in German may also have contributed to the apparent lack of knowledge of each other’s papers, though Debauche did cite Soyka’s earlier papers, none of which contained *Anaphes* species descriptions, and Soyka (1955) did criticize Debauche’s (1948) choice of *fuscipennis* as the genotype of *Anaphes*. Debauche claimed that he could not recognize any of the [previously] described species, yet he redescribed four of them, *fuscipennis*, *pratensis*, *flavipes* and *autumnalis*, based on material collected by him. Debauche evidently put considerable emphasis on phenology, noting carefully in what months he collected the specimens. His specimens of *fuscipennis*, collected from August to October, and *pratensis*, collected in April, were both misidentified. While we are not certain what species his *fuscipennis* belong to, his *pratensis* specimens clearly are *fuscipennis*, as shown by his drawing of the female antenna. Moreover, *fuscipennis* may be collected both in early spring and late autumn, suggesting either that it has at least two generations per year or that the individuals developing in some of the parasitized eggs remain dormant (aestivation) until the autumn when they emerge. Aestivation of a small percent of the eggs also occurs in *diana* (Aeschlimann 1977).

Debauche produced a detailed genus description and exhaustive species descriptions but word by word study of these shows that most of the features are described in terms that are either too vague to be of any use for *Anaphes*

species identification or are so general that they apply to almost any species of Mymaridae. The vagueness is not entirely Debauche's fault. It is almost impossible to describe accurately features such as fore wing or gaster shape in absolute terms. There are several good points to Debauche's descriptions, however—he gave absolute measurements for body, wings and antenna (length only, unfortunately) of the holotype and a male paratype if males were described [at least one male, the allotype of *calvescens*, is clearly not conspecific with the female; it is either a specimen of *brevis* or of *collinus*]; he compared his species with others and gave what he considered to be diagnostic features; he described the flight period and habitat or microhabitat in which he collected his specimens; and he illustrated with accurate line drawings the fore wing and female antenna of all the species and the gaster, metatarsus and base of the antenna (usually pedicel–fl<sub>2</sub>) for several. His emphasis on setation of the scape–fl<sub>2</sub> and fore wing venation seems excessive and needs to be evaluated more thoroughly across all species and for longer series of specimens of each species to determine their taxonomic value. Debauche (1948: 11) stated that mymarids have weak active dispersal powers so the species found along irrigation ditches, for example, are generally different from those found only a few metres away from those ditches. In our view Debauche placed too much emphasis on habitat or microhabitat. For parasitoids, the habitat or microhabitat are poor substitutes for a particular host association. Debauche also placed considerable emphasis on collecting dates. But some species have several generations per year so collecting dates are not necessarily very helpful. The hosts themselves may occur across more than one habitat, depending on where their host plant(s) occur and even if active dispersal is limited, passive dispersal is clearly not. Besides, as Soyka (1949) explained, most of Soyka's specimens were collected at windows, including one 15 m high in a student residence. This clearly indicates that *Anaphes* specimens (and those of other genera as well) are blown around and therefore may move considerable distances before landing somewhere else that may contain suitable hosts. So Debauche probably overestimated how closely associated a given *Anaphes* species is to a particular type of habitat and this likely influenced how he determined the number of species he described. Kenis *et al.* (2003), however, showed that *Anaphes* sp. may be reared from lily leaf beetle eggs, but only those collected exclusively from forested areas, indicating that this *Anaphes* species, at least, is habitat restricted.

Debauche's keys to *Anaphes* spp. have fewer absolute features than the couplet lengths suggest. In both his *A. (Anaphes)* and *A. (Patasson)* keys he mainly used proportions of female antennal segments and distribution of mps, wing shape, measurements and colour, wing surface setation (number of microtrichia rows), gaster shape, ovipositor length and degree of its extension under the mesosoma, and metatarsomere lengths. Debauche's collection (IRSNB) contains many more slide-mounted *Anaphes* that are unidentified compared to the few specimens that he named and described, suggesting that he could not distinguish them and therefore included in his type series only those specimens that seemed to be most distinctive from other series of specimens. For only one species, *dorcas*, Debauche mentioned some variation but he didn't discuss it because he stated he had too few specimens. The same problem thus arises as in Soyka's keys and partly for the same reason, that intraspecific variation was not sufficiently taken into account due to the small number of specimens recorded in each of his species descriptions (perhaps regardless of how many more specimens Debauche may have examined but not included).

From all the above it must be concluded that host range, phenology, geographic distribution, habitat or microhabitat, and sometimes even morphology or host species are insufficient to identify confidently to species a given specimen of *Anaphes*, particularly those found in Europe. Other evidence obtained from the specimens themselves is needed. The most useful at present would be information from DNA sequencing. Until many specimens representing several morphospecies are studied with this technique it is unknown how well it will work to distinguish the species. Conversely, it may also show that certain species described from Europe are the same as those described from some other region, particularly North America. How molecular information will eventually be correlated correctly with nominal species based only on slide mounted specimens remains to be determined. We (particularly the junior author) tried to match many of the specimens reared from known hosts (Table 7) with the images of *Anaphes* type specimens, and he was mostly unable to arrive at definite answers as to the species involved.

After briefly explaining changing mymarid species concepts over time and the problem of applying them to European *Anagrus* species, Chiappini (1989) pointed out the need, faced by any taxonomist, to examine critically any relevant primary type specimens to determine the correct application of names. This is, of course, unavoidable in most cases because the type specimen is often the only known representative of a published nominal species and the original descriptions themselves are often hopelessly inadequate for use in identifying a species. Although

Chiappini chose to avoid placing any *Anagrus* species in synonymy that had even a small morphological difference, perhaps in only a single character, she nevertheless produced quite an extensive list of synonyms of Soyka's *Anagrus* species.

For *Anaphes*, we are less restrictive than Chiappini, knowing that:

- a) There may be considerable discrete morphological variation within a given *Anaphes* species (Huber & Rajakulendran 1988) as well as large ranges of continuous variation in measurements or ratios. For example, Santolamazza-Carbone *et al.* (2007) showed that wing length in *nitens* can vary up to 36%, and Gahan (1927) and Huber (1992) showed that the largest specimens of *calendrae* may be over twice as long as the smallest, when reared from different hosts. Sveum & Solem (1980) measured 50 females and 10 males of *crassipennis* (as *cultripennis* in their paper) from Norway to show the amount of variation in the lengths of body, metatarsus, and antennal segments. Unfortunately, they did not give ranges, only standard deviation from which approximate ranges can be obtained by multiplying by four (a rule of thumb calculation). Thus, their fore wing width measurement for females of 0.183 mm with SD 0.030 gives a range of  $\approx 0.123\text{--}0.243$  and about 50% difference between the narrowest to the widest wing.
- b) For many Soyka species it is highly unlikely that many different *Anaphes* species, e.g., 30 at Hundsheim, 40 at Valkenburg, would be collected from a window or windows in a single building at each locality over only a few months over one or two years, particularly as most of them came from the same type of habitat (fields or meadows).
- c) Aeschlimann (1986, 1990) showed that in *diana*, a widely distributed European species introduced into North America for biological control purposes, both bisexual and unisexual forms were identified and occurred sympatrically in Europe. Though no morphological differences could be found between the two biotypes, electrophoretic differences were found. Unfortunately, no morphological studies were done to test if geographical variation also occurred. Unisexual specimens by definition represent their own evolutionary lineages (no genetic mixing across two or more generations) and may show greater differences, morphologically or otherwise, than in bisexual specimens of the same species. If these unisexual forms are collected they may appear so different from one another that they are described as different species. Unisexual lineages may also occur in other *Anaphes* species and if any of the females could opportunistically parasitize hosts outside their normal host range that might lead to fixed differences in size or other morphological features.

Phenotypic and other types of variation is also well documented in other genera of Mymaridae, e.g., Segoli & Rosenheim (2015) for metatibia length in one species of *Anagrus*, and in other families of egg parasitoids, e.g., Boivin (2010) and Abram *et al.* (2016, and references therein) discussed variation in various feature due to host, phenology, etc. Johnson *et al.* (1987) showed that host-related antennal variation occurs in a polyphagous egg parasitoid, *Telenomus alsophilae* Viereck (Platygastridae, Telenominae). Popovici *et al.* (2011) discussed variation for *Triteleia* sp. (Platygastridae, Scelioninae). Medal & Smith (2015) demonstrated significant differences in body weight and length in *Trissolcus japonicus* (Ashmead) (Scelioninae) reared from different sized host eggs of three species of Pentatomidae (Hemiptera). Considerable plasticity in morphological or other characters evidently occurs widely in small parasitic Hymenoptera, which complicates species recognition and makes it more difficult to prepare meaningful taxonomic descriptions.

The Pleistocene Epoch began 2.588 million years ago. The last maximum extent of the Pleistocene glaciation is widely accepted to be around 18,000 years before the present. Ice covered all of Scandinavia, most of Great Britain, northern Germany (up to 200 km inland from the current Baltic Sea) and Poland (in the western part, extending south to the latitude of Warsaw), and all of the Alps area but not eastern Austria (Ehlers & Gibbard 2004, and chapters therein). Unglaciated areas occurred in southern England and Ireland, and across mainland Europe, south of the Fennoscandian ice cap, to the Caspian Sea. The ice-free corridor was narrowest north of the Alps. The vegetation there was tundra and, further south, steppe vegetation but coniferous and some deciduous trees may have survived in some refugia. Southern Europe (most of the Iberian Peninsula, western France, most of Italy and southeastern Europe) was apparently ice free. If *Anaphes* specimens did not manage to survive what may have been too harsh a climate between the Alpine and northern icecaps during the glacial period, they must have recolonized the north either from southern Europe or from the east (Near and Middle East and north of the Black Sea), though perhaps some survived in western France. But it seems unlikely that all the nominal species describe so far for Europe already existed in the southern and eastern areas, and successfully recolonize central and northern Europe.

It is also unlikely that they could have evolved morphologically recognizable specific differences since the last glaciation(s) though if unisexual lineages colonized recently unglaciated habitats further north this may have resulted in faster speciation, or at least allowed for less gene flow among populations and, possibly, greater variation among them depending on what the hosts were. Regardless of what may have occurred in *Anaphes* in Europe over the past few million years we believe there were and still are far fewer species than Soyka and others described.

If one compares the European (or Palearctic) and North American *Anaphes* fauna with the fauna of the Australian region, most of whose species are undescribed, the relative uniformity of the former contrasts strikingly with the relative diversity of the latter, e.g., in wing shape and pattern, and in body sculpture. The *Anaphes* fauna of the Afrotropical, Neotropical, and Oriental regions is still poorly known so we cannot make meaningful comparisons but from the relatively little material examined it seems that the *Anaphes* species in those areas may also be more diverse morphologically than in Europe. All those regions were not or, at most, only slightly glaciated during the Pleistocene. Yet their *Anaphes* fauna appears to be far less speciose than in Europe. Even though this is partly due to lack of collecting, it strongly suggests that the European fauna is greatly overdescribed.

A major problem is to have many nominal species of *Anaphes* that are poorly characterized because each is based on only one or, occasionally, a few slide-mounted specimens. They can only be studied morphologically in one orientation and with difficulty because most slide-mounted specimens in collections are uncleared. Although most Soyka specimens are mounted in lateral view, which is important for measuring the ovipositor length (or ovipositor sheath length, which is easier to see and almost identical) and seeing how far under the mesosoma it extends, it would be useful also to have specimens mounted in dorsal view. Because most of Soyka's species are based on one specimen this is obviously not possible and, of course, intraspecific variation in those nominal species cannot be assessed. We conclude that there are at most about 35 morphologically recognizable *Anaphes* species in Europe, not the 190+ recognized by Soyka and others. And we certainly do not believe that the species that survived through the last glaciation in southern or eastern Europe and later migrated north diversified into the large number of named species recognized previous to the present work.

If we wait for freshly collected specimens and biological information on reared specimens that can somehow be matched with one or more of Soyka's nominal species nothing would likely be done on *Anaphes* for many more decades. Besides, the additional information would not actually solve the problem of determining which European *Anaphes* species are synonyms of one another because none of Soyka's specimens were reared from known hosts and DNA is almost certainly not obtainable from his slide mounted specimens. Because so many of his species are described from single specimens it is a totally arbitrary decision to determine if two specimens differ enough to be treated as different species or the same species. We have taken the view that there is far more intraspecific variation than Soyka or perhaps even Debauche imagined, hence the numerous synonyms proposed for most of their species. If some enterprising individual would like to remeasure all of Soyka's 900 named *Anaphes* specimens (mostly paratypes, many of which were invalidly designated) and do some statistical analyses they may well come up with a different number of species and synonyms or find that we misplace some synonyms under the wrong senior synonym. We may even have placed too few species in synonymy. There is no assurance that any of Soyka's paratypes, particularly the male specimens, actually belong to the same species as the corresponding holotypes so detailed analyses based on measurement of paratypes may be useless for species identification, though perhaps not for clustering specimens into distinguishable groups.

Cryptic species of *Anaphes* exist and although almost identical morphologically they differ in biology (Huber *et al.* 1997). Conversely, significant morphological differences may occur in specimens reared from different hosts (Huber & Rajakulendran 1988). Finally, although relatively few *Anaphes* species were described from North America, several of these are very likely the same as European species but described under one or more different names. Resolving these synonymies more satisfactorily than we did will necessitate comparison of fresh material from both continents using a variety of techniques. Whether they can ever be confidently assigned a correct species name is uncertain, as Huber (2015b) discussed for *atomarius*. However, based on morphological comparison of the type specimens we have been able to synonymize fairly confidently many of the existing nominal species. We stress, however, that our results are preliminary because of the limitations imposed by the material for study. Numerous card or point mounted *Anaphes* specimens have accumulated in several North American (CNC, UCRC) and European collections, e.g., BMNH, and several collections have material (often reared) on slides e.g., BMNH, DEI, DEZA, IRSNB, ZMUC. Careful study of all this material to determine the species, their limits and their

distributions would be desirable to provide a better foundation for a European *Anaphes* revision, assuming that DNA can first be extracted from the specimens before preparing good slide mounts. A thorough revision of *Anaphes*, particularly in Europe, based on fresh material, preferably using new techniques such as molecular analysis is a long term effort that is required to resolve (we hope) the problems mentioned above. A better knowledge of *Anaphes* species may potentially also further their use for biological control. We challenge the enterprising and industrious, perhaps even masochistic, future student of Mymaridae to re-examine our conclusions by studying and perhaps measuring again all of Soyka's types, both primary and secondary, as well as other material from various European and North American institutions, to see if our synonymies are correct.

For whatever reason, some people are or become compulsive describers of specimens that they then glorify as species. Taxonomists, whether professional or amateur, all describe specimens as a proxy for species but usually with a more or less sound rationale for doing so and they usually do not become extreme splitters. But for some, describing and naming new species seems to be an obsession and their scientific justification for doing so is weak or non-existent. The most notable of such people in the 1800s is perhaps Francis Walker (1809–1874) though criticism of his work is unjustifiably harsh (Evenhuis 2011). But there are others, publishing on a variety of taxonomic groups, who have also been describers of large numbers of species of dubious status so their work will have to be carefully reassessed. If one compares Soyka to the two other prolific describers of Mymaridae in the 1900s, A.A. Girault and A.A. Ogloblin, the latter two were essentially playing Linnaeus because they worked, respectively, in North America and later in Australia, and in southern South America, three regions that were previously unexplored for Mymaridae so most of their species remain valid (less so with their genera, incidentally). In contrast, Soyka was working in Europe, the most depauperate continent for Mymaridae, where 18 *Anaphes* species had already been described before Soyka's 1946a and 1946b papers (which included 11 new species) then another 14 species described by Debauche (1948) before Soyka described all his remaining species.

The junior author curated the Enoch and Waterhouse collection of Mymaridae (BMNH) and found 47 manuscript names on the card- or slide-mounted *Anaphes* (thankfully, none of them were published) and reclassified these into about 18 species as more or less recognized by us, including quite a few that could not be placed confidently to species. Thus, Soyka was by no means the only splitter for Mymaridae but he created most of the problems—first, because he actually published his names and, second, because his proportion of valid species (as determined by us, at least) is so low, considerably lower, for example, than by various dipterists who described species in the 1800s (Evenhuis 2011: 33, 39). Even though Soyka published his species in the mid 1900s his thinking could fit very well the 19<sup>th</sup> century Victorian naturalist approach to describing species (Barber 1980). In chapter 4, Barber quotes Charles Kingsley “The truth is, the pleasure of finding new species is too great; it is morally dangerous; for it brings the temptation to look on the thing found as your own possession, all but your own creation; to pride yourself on it, as if God had not known it for ages since; even to squabble jealously for the right of having it named after you, and of being recorded in the Transactions of I-know-not-what Society as its first discoverer.”

## Conclusions

We have spent considerable time trying to sort out Soyka's nominal species of *Anaphes*. While our synonymies may not all be correct we hope that what we have accomplished will result in greater attention being paid to *Anaphes* taxonomy and biology. If not, we hope at least that our tabular summaries of names will alleviate the tedium others would face of going through all the past literature again to organize the 231 *Anaphes* nominal species, let alone redescribing, with new evidence, e.g., molecular, those they consider valid.

Despite there being a finite number of species in the present (Quaternary) geological period (a much earlier and evidently more diverse fauna existed in the Cenozoic or Tertiary period, as shown by Baltic amber fossils), specimen describers such as Soyka and others guarantee that the production of extant “species” descriptions will be endless. One could thus paraphrase Ecclesiastes 12:10 (the Bible): “Of the making of many books there is no end, and much study is a weariness of the flesh” with “Of the describing of many species there is no end and much study to determine their identity and synonymies is a weariness of the flesh.” Some specimen describers—“taxonomists” in a loose sense—perhaps suffer more from vanity than others but the end result for much of what we taxonomists all do, and to varying degrees are guilty of, may be summarized thus: “Vanity of vanities, says the Preacher, all is vanity (Ecclesiastes 12: 8).

## Acknowledgements

We thank the following curators for help: D. Zimmermann (NHMW) for permission to examine the Soyka types during our visits to Vienna and for the loan of all Soyka material to the junior author for study and photography. The senior author thanks A. Touret-Alby (MNHN) for searching (unsuccessfully) for the types of *peyerimhoffi*, B. Landry (MHNG) for loan of Soyka paratypes of *Anaphes* deposited in Geneva, M. Gates (USNM) for loan of Girault types, J. O'Connor (NMID, retired) for loan of three Haliday types, C. Schmidt (CNC) for help with translation of some of Soyka's more difficult German sentences and specimen labels and, A. Gehler, Geoscience Centre, University of Göttingen, Germany, for drawing attention to the fossil specimen labelled as *Anaphes splendens*. K. Bolte (CNC, retired) prepared the SEMs of *Anaphes* and J. Read (CNC, retired) added the abbreviations of morphological structures to the SEMs, photographed all the slide-mounted specimens other than the primary types of Soyka and Debauche, and compiled the images into plates. The Soyka type plates were prepared by S. Bancsó, Jurisich Miklós High School (Kőszeg, Hungary). Images of the teratological specimen were kindly supplied by S. Triapitsy (UCRC). One reviewer and the subject editor provided excellent comments and criticism of the manuscript. Their input helped greatly in improving it.

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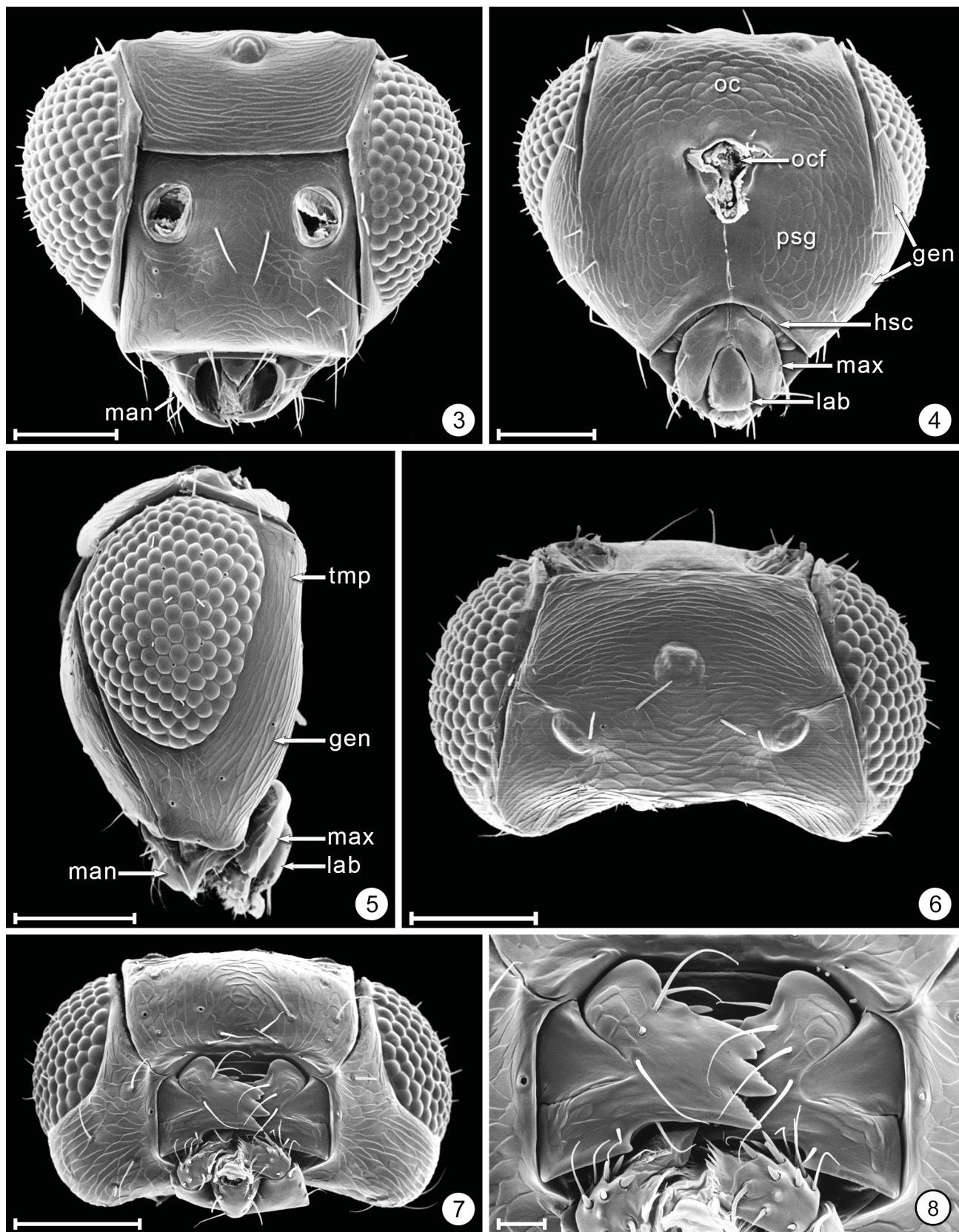
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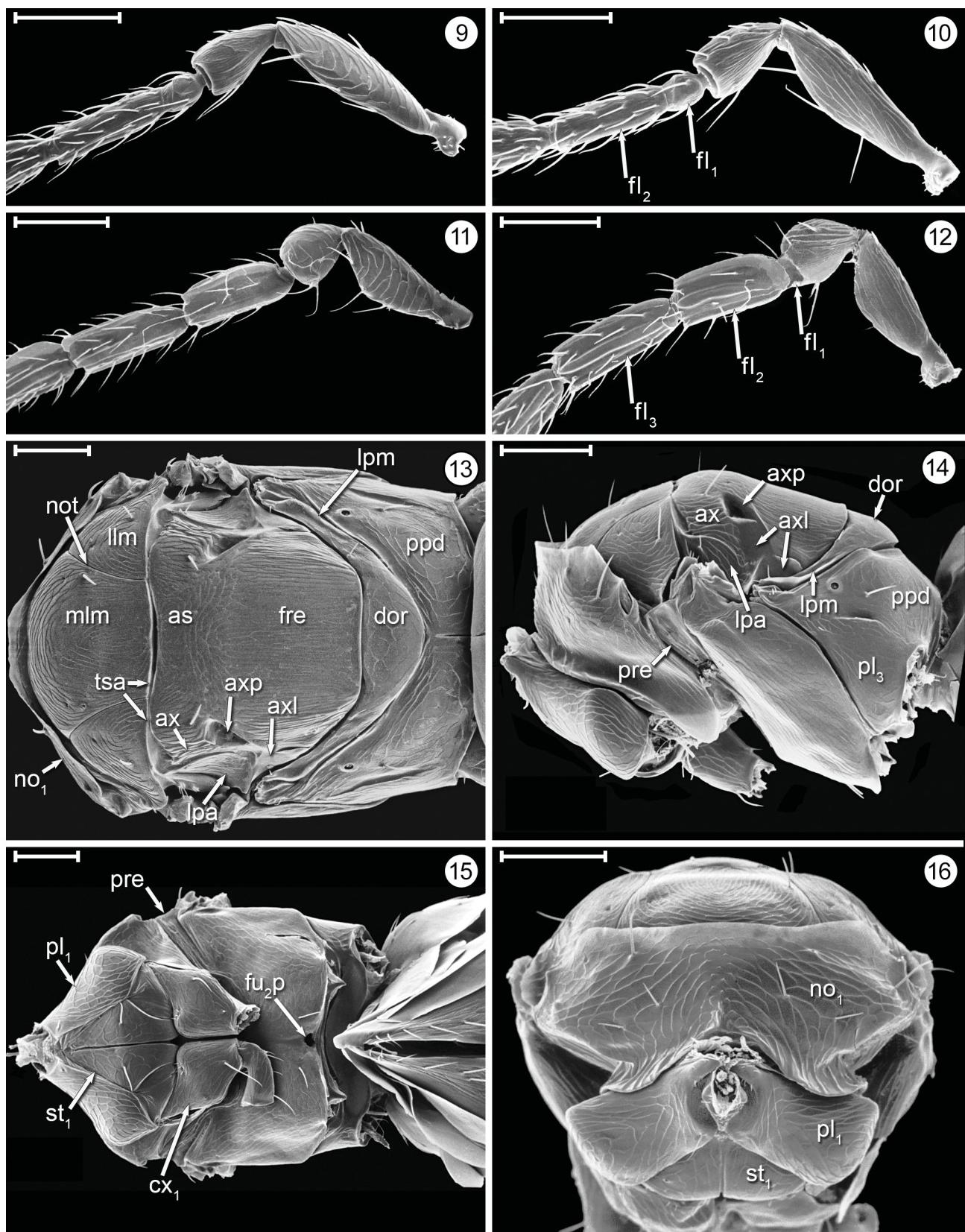
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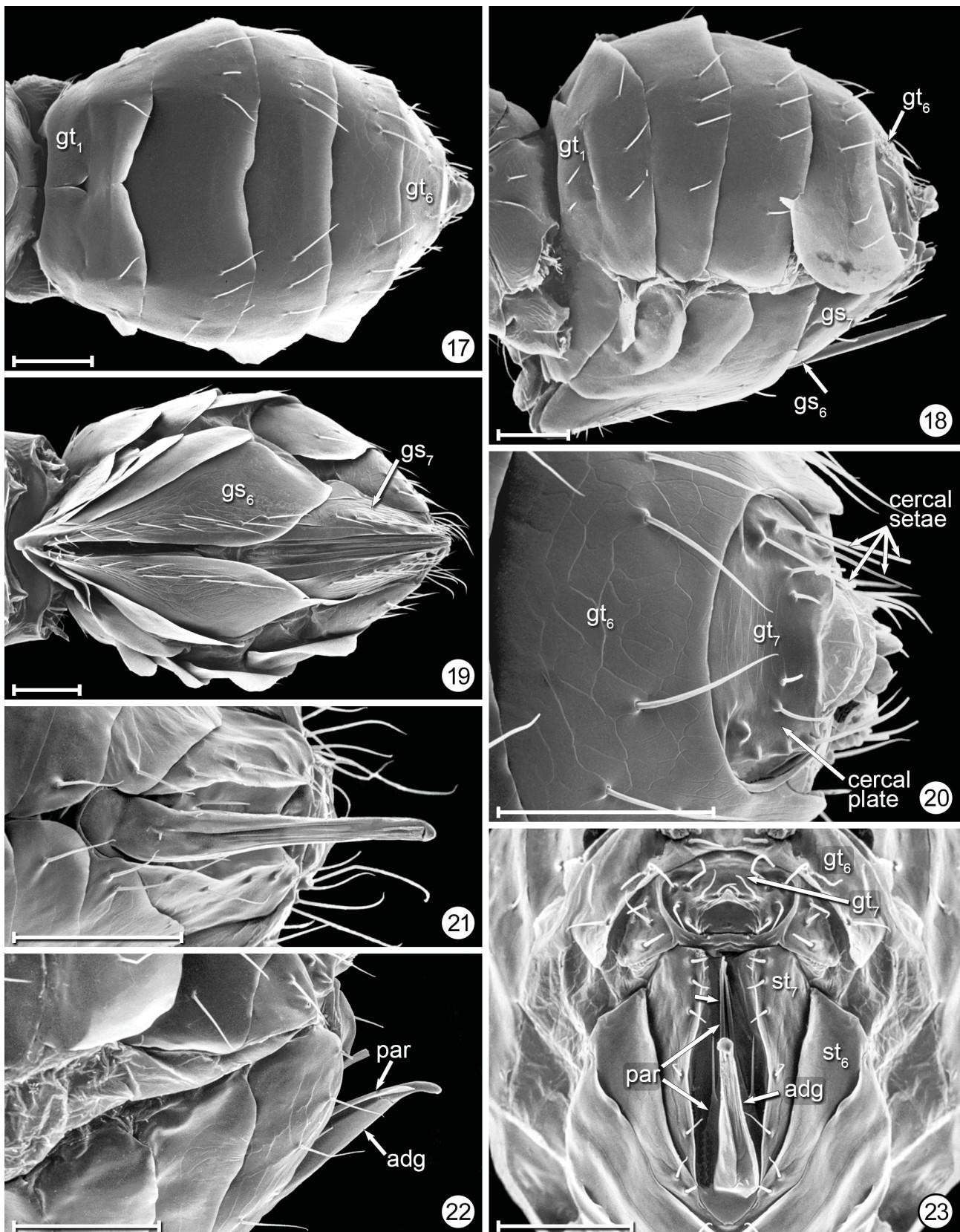
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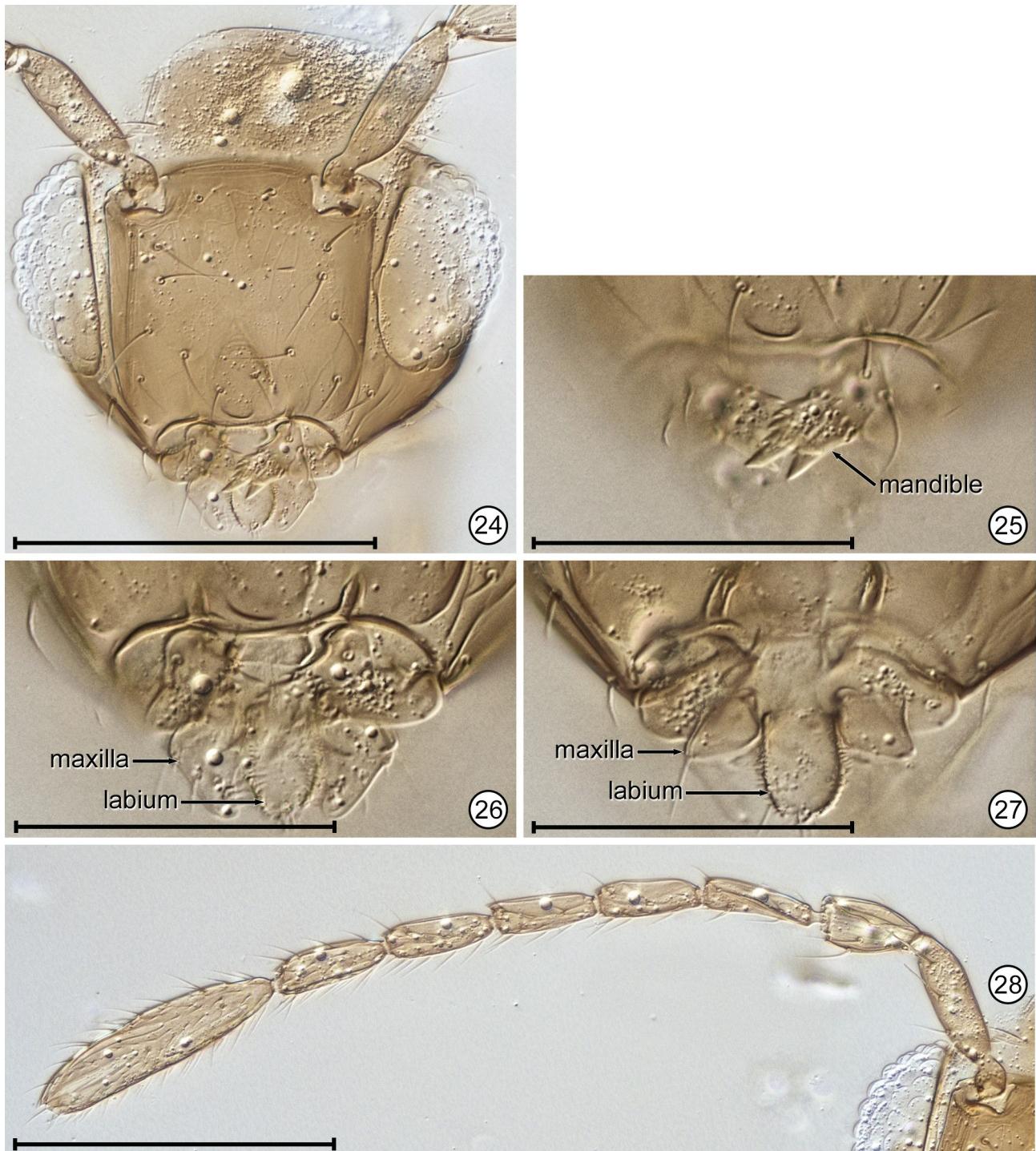
**FIGURES 3–8.** *Anaphes* sp., micrographs of head of unidentified specimens from Canada. 3, anterior; 4, posterior; 5, lateral; 6, dorsal; 7, ventral; 8, mouthparts. See Table 8 for morphological terms. Scale bars for 3–7 = 50 µm, for 8 = 10 µm.



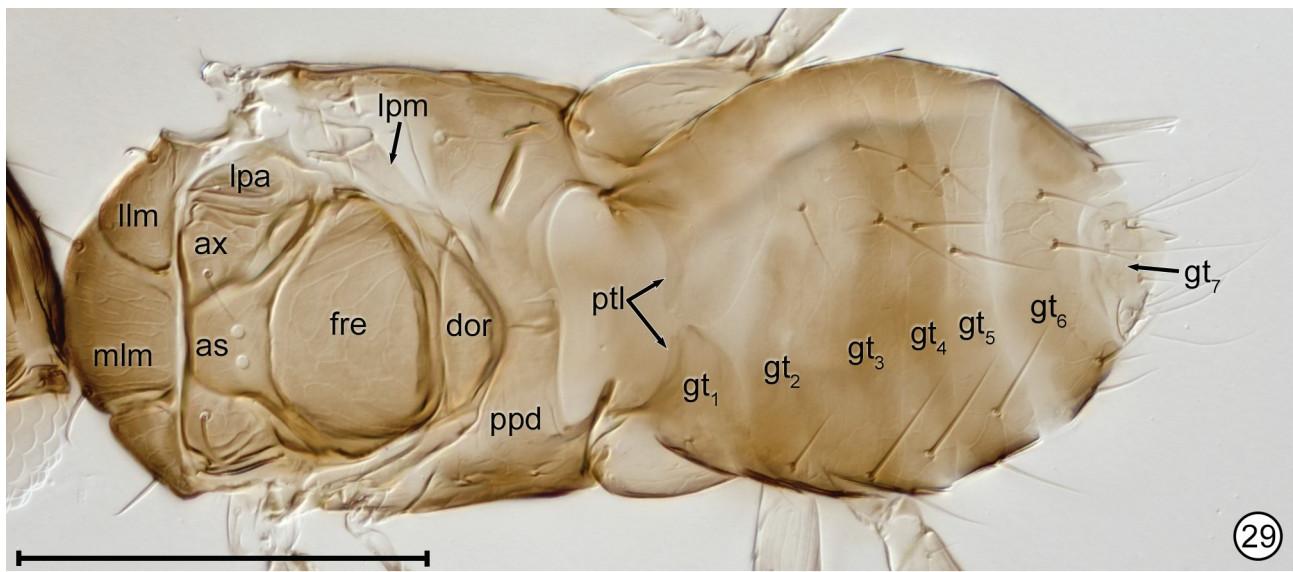
**FIGURES 9–16.** *Anaphes* sp., micrographs of unidentified specimens from Canada. 9, female, scape–base of fl<sub>3</sub>, inner (medial) surface; 10, female, scape–base of fl<sub>3</sub>, outer (lateral) surface; 11, male, scape–base of fl<sub>4</sub>, inner (medial) surface; 12, male, scape–base of fl<sub>4</sub>, outer (lateral) surface; 13, mesosoma, dorsal; 14, mesosoma, lateral; 15, mesosoma, ventral; 16, mesosoma, anterior. See Table 8 (p. 50) for morphological terms. Scale bars = 50 µm.



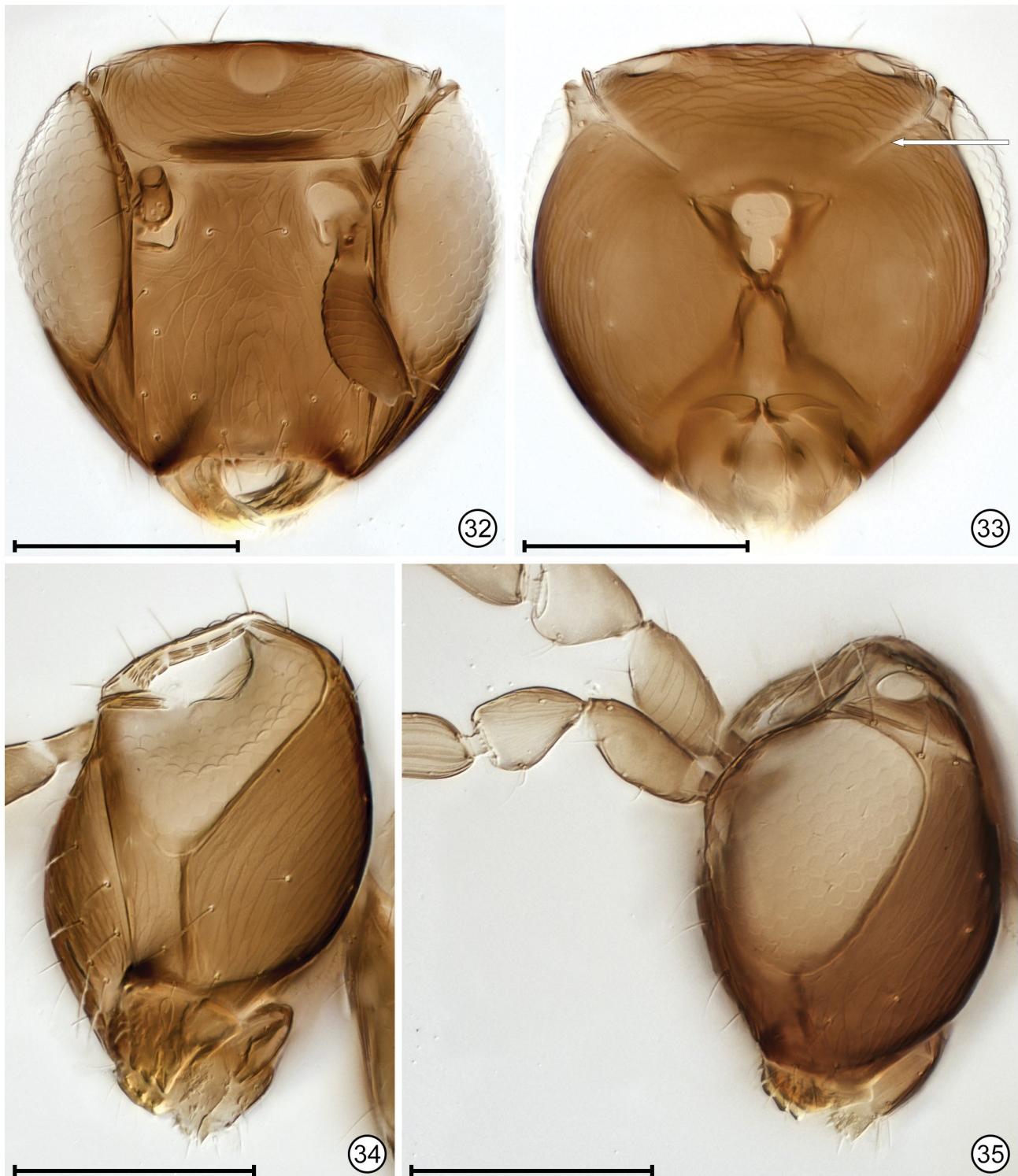
**FIGURES 17–23.** *Anaphes* sp., micrographs of unidentified specimens from Canada. 17, female, metasoma, dorsal; 18, female, metasoma, lateral; 19, female, metasoma, ventral; 20, male, apex of metasoma, dorsal; 21, male, genitalia, ventral; 22, male, apex of gaster, lateral; 23, male, apex of gaster, posterior. Scale bars = 50 µm.



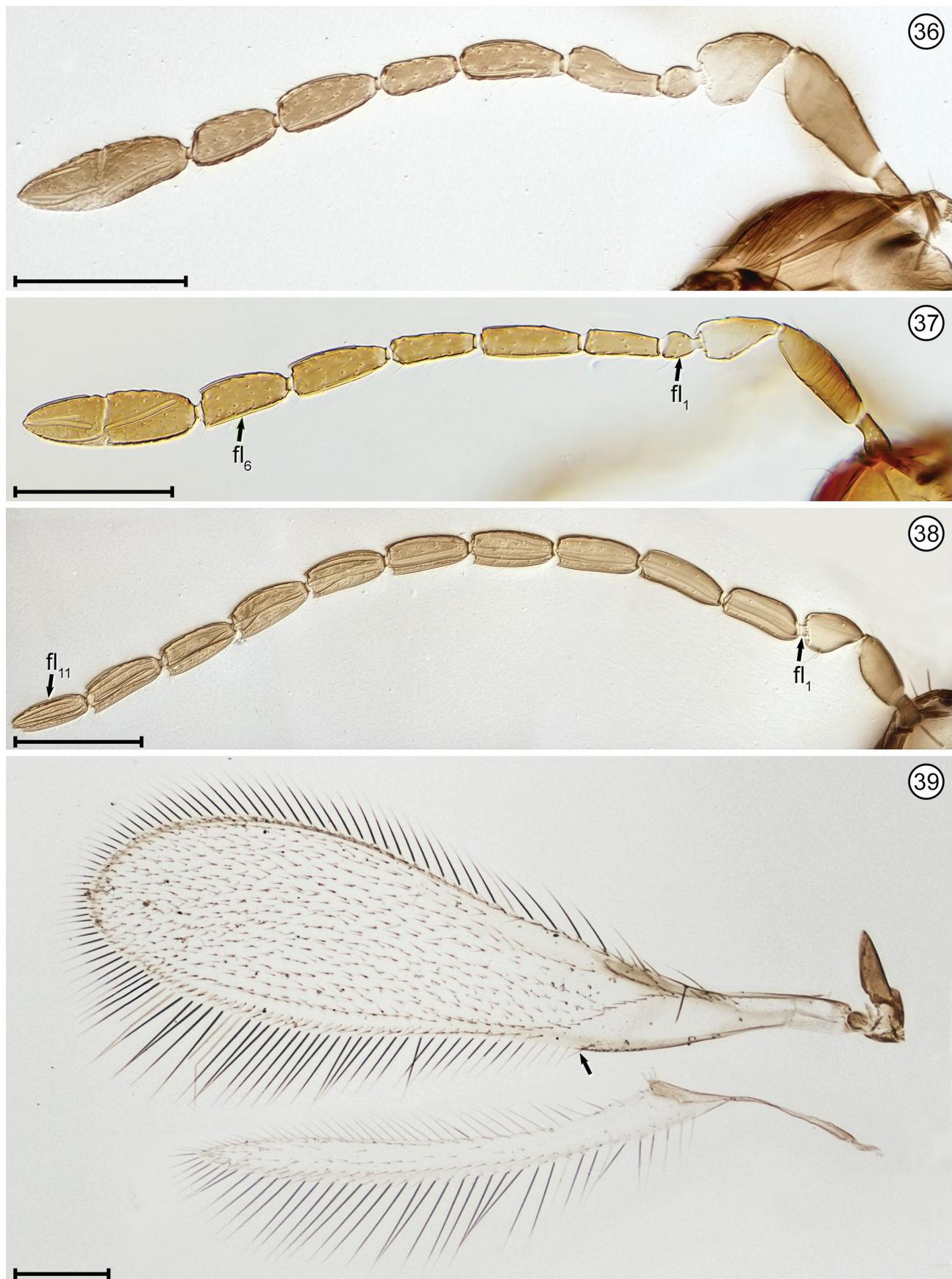
**FIGURES 24–28.** *Anaphes quinquearticulatus*, paratype female. 24, head, anterior; 25, mouthparts, left mandible in focus; 26, mouthparts, maxillae in focus; 27, mouthparts, labium in focus; 28, antenna. Scale bars for 24 and 28 = 100 µm, for 25–27 = 50 µm.



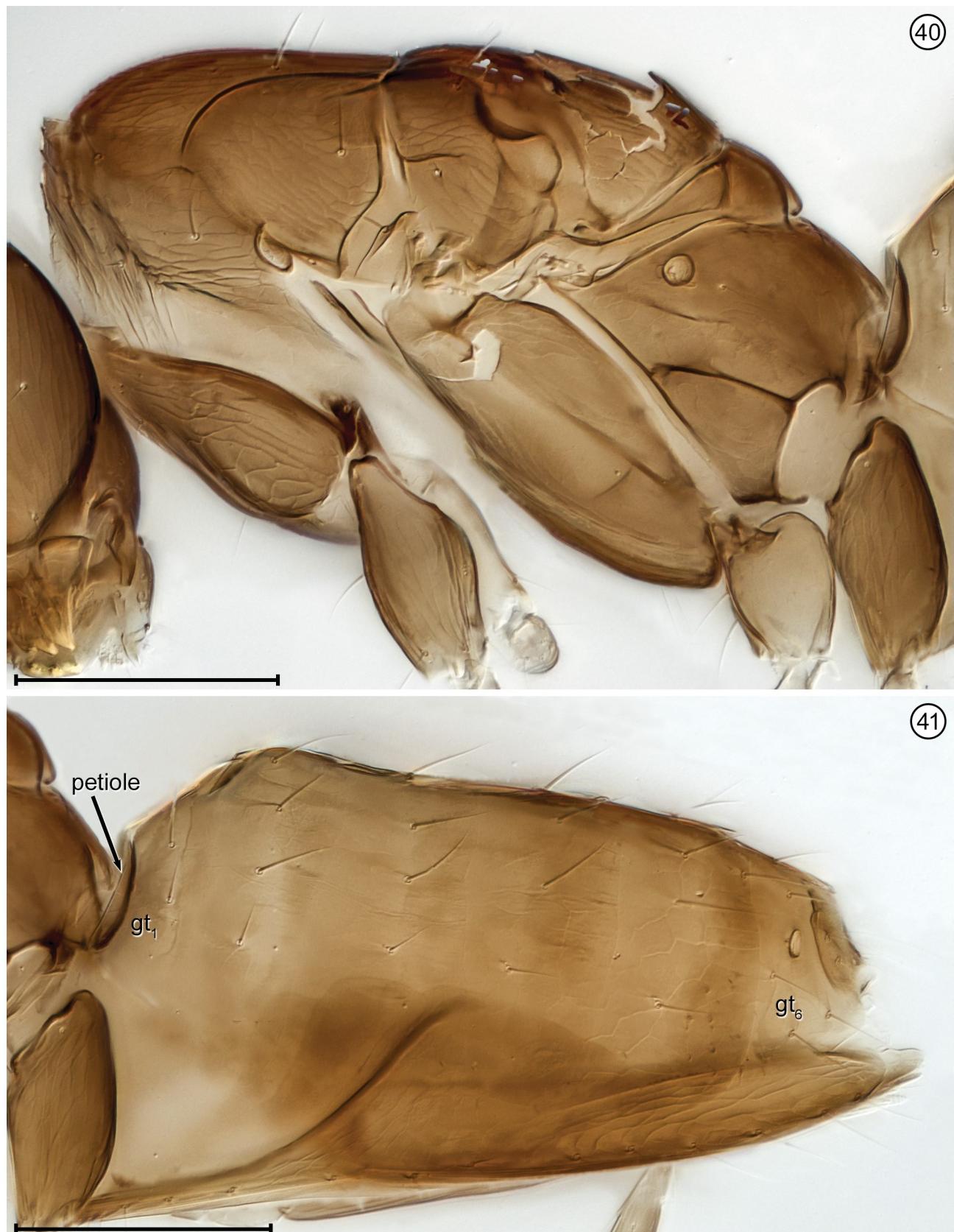
**FIGURES 29–31.** *Anaphes quinquearticulatus*. 29, paratype female, mesosoma + metasoma, dorsal surface; 30, paratype female, mesosoma + metasoma, genitalia as seen through body; 31, holotype wings. Scale bars = 100 µm.



**FIGURES 32–35.** *Anaphes brevis*, head, specimen from Spain, Catalonia, Navata, emerged 21.ix.2000 ex. *Lygus* eggs on *Chenopodium* (in cages 14–21.ix.2000), D. Coutinot & J. Lopez. 32, anterior; 33, posterior—arrow indicates vertexal suture (incorrectly named the occipital suture in Huber 2006, fig. 32); 34, slightly ventrolateral; 35, slightly dorsolateral. Scale bars = 100 µm.



**FIGURES 36–39.** *Anaphes brevis*, Same collection data as in Figs 32–35. (except Fig. 39—France, Yvelines, Béhoust, vi.1987, lab. culture ex. *Lygus*). 36, female, left antenna (outer surface); 37, female, right antenna (inner [medial] surface); 38, male, left antenna; 39, wings—arrow indicates socketed seta at apex of retinaculum. Scale bars = 100 µm.



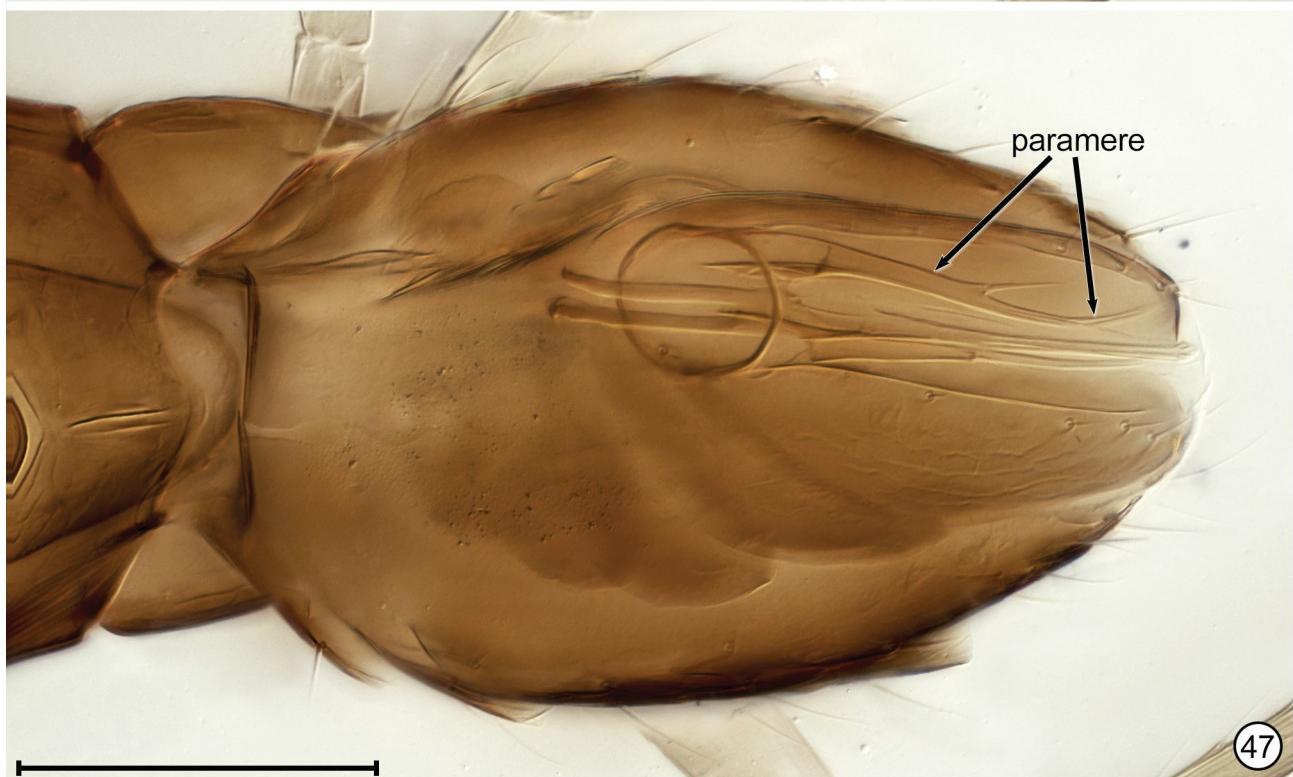
**FIGURES 40, 41.** *Anaphes brevis*, female, same collection data as Figs 32–35. 40, mesosoma, lateral; 41, metasoma, lateral. Scale bars = 100 µm.



**FIGURES 42, 43.** *Anaphes brevis*, same collection data as Figs 32–35. 42, female, metasoma, lateral, showing genitalia; 43, male, mesosoma, dorsal. Scale bars = 100 µm.



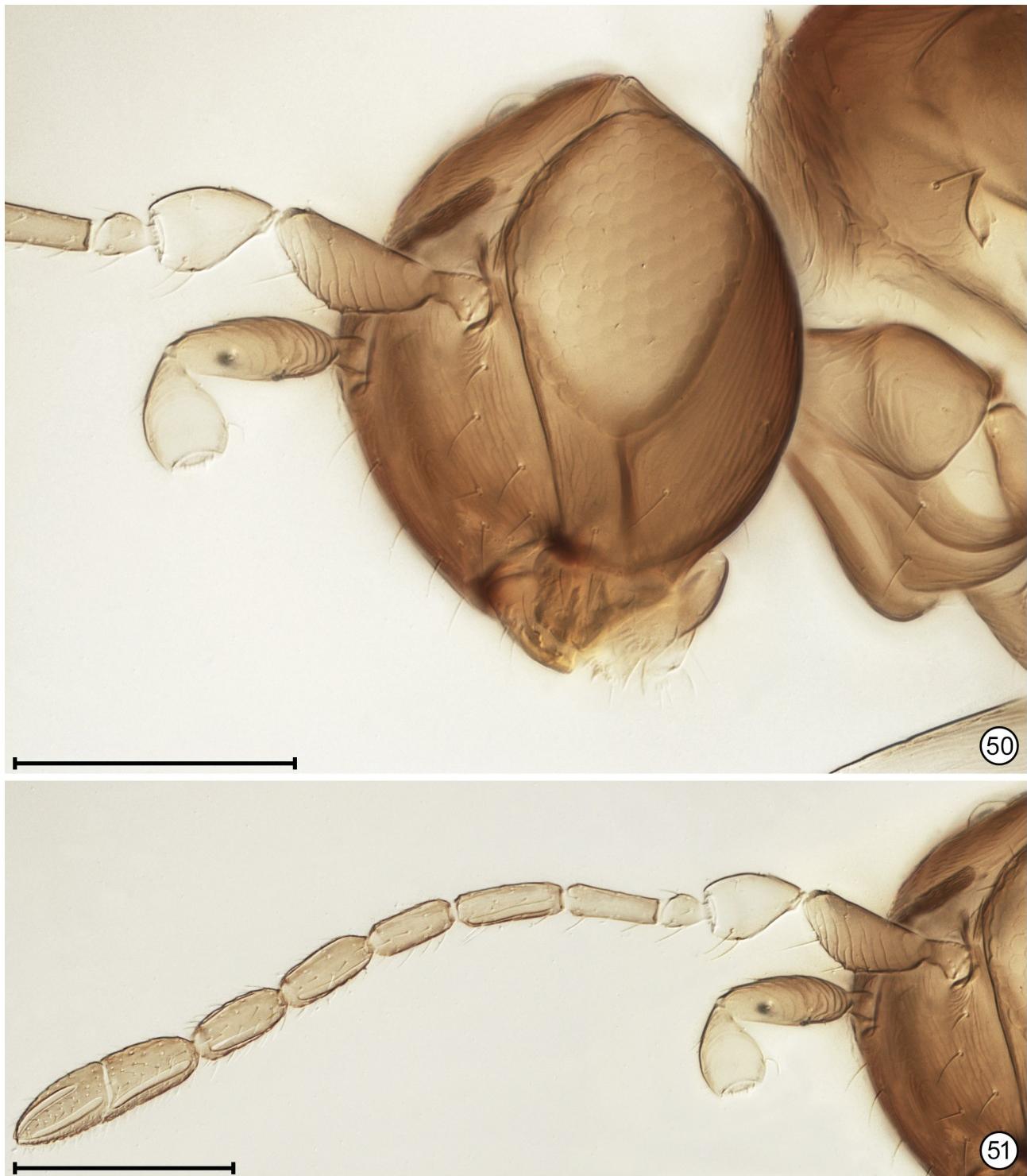
**FIGURES 44, 45.** *Anaphes brevis*, male, same collection data as Figs 32–35. 44, mesosoma, lateral; 45, legs, lateral—tarsomere lengths measured from one insertion to the next, as indicated by arrows. Scale bars = 100 µm.



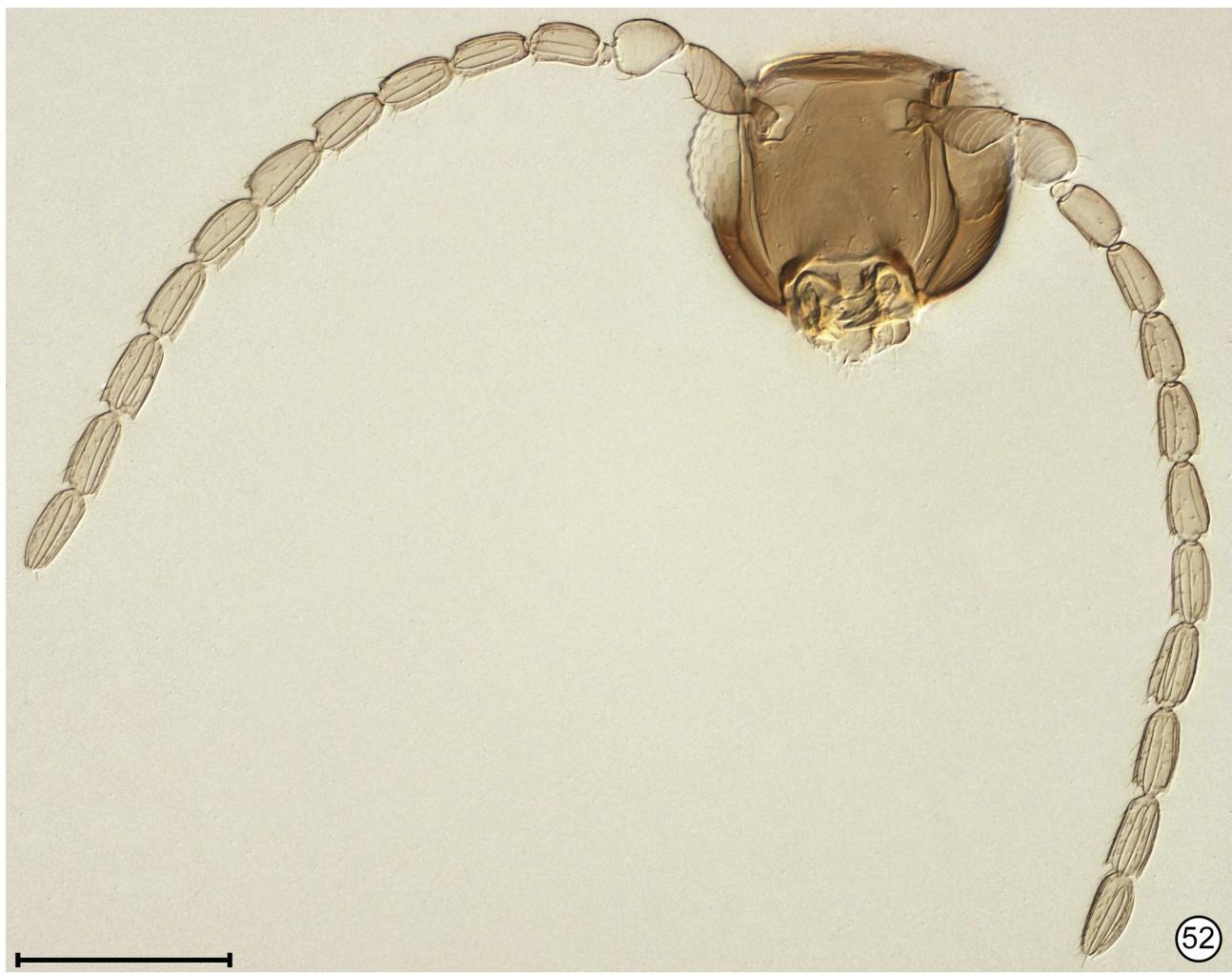
**FIGURES 46, 47.** *Anaphes brevis*, male, same collection data as Figs 32–35. 46, metasoma, dorsal; 47, genitalia, dorsal, as seen through metasoma. Scale bars = 100  $\mu$ m.



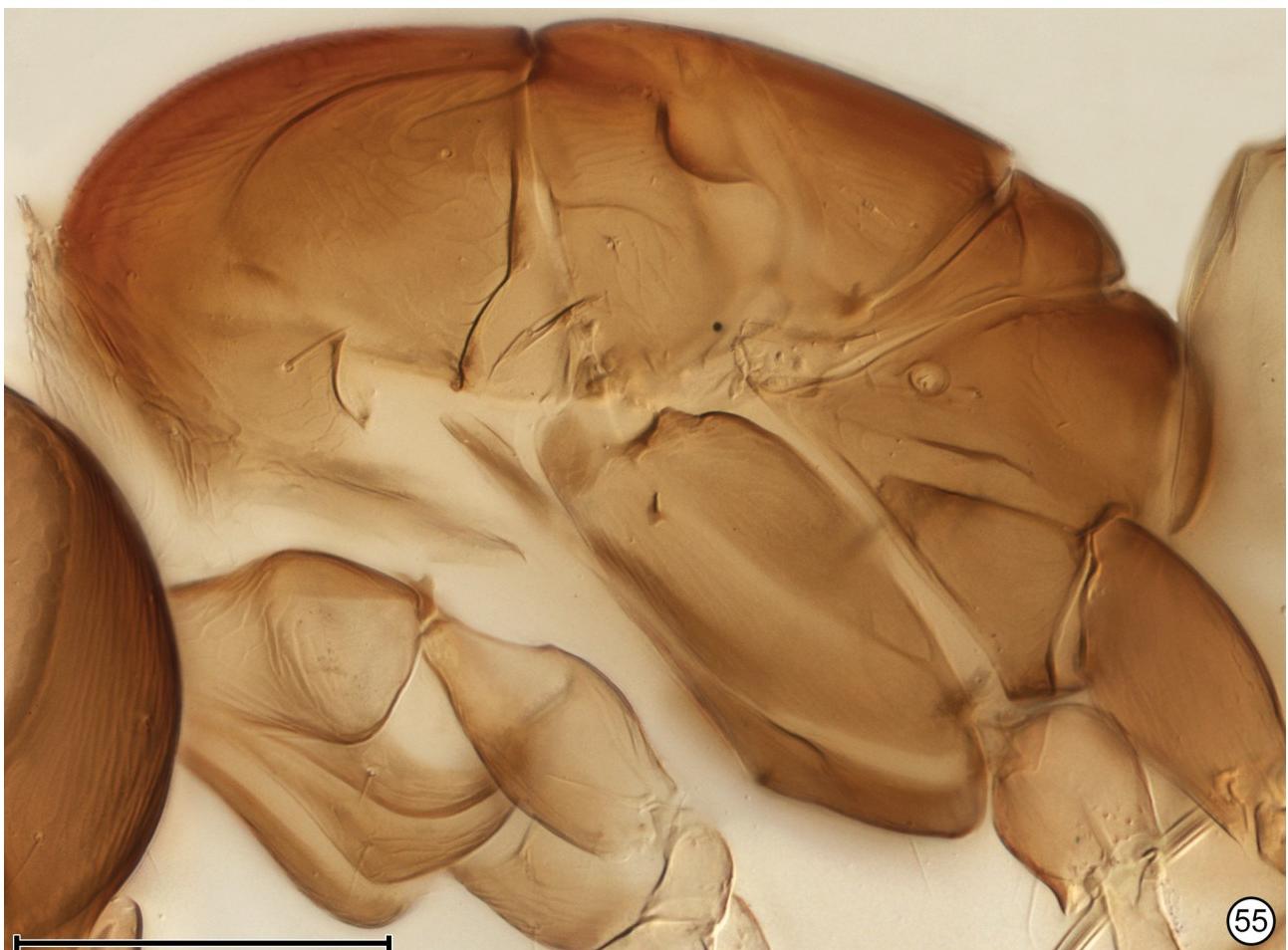
**FIGURES 48, 49.** *Anaphes brevis*, male, same collection data as Figs 32–35. 48, metasoma, lateral; 49, genitalia lateral, as seen through metasoma. Scale bars = 100 µm.



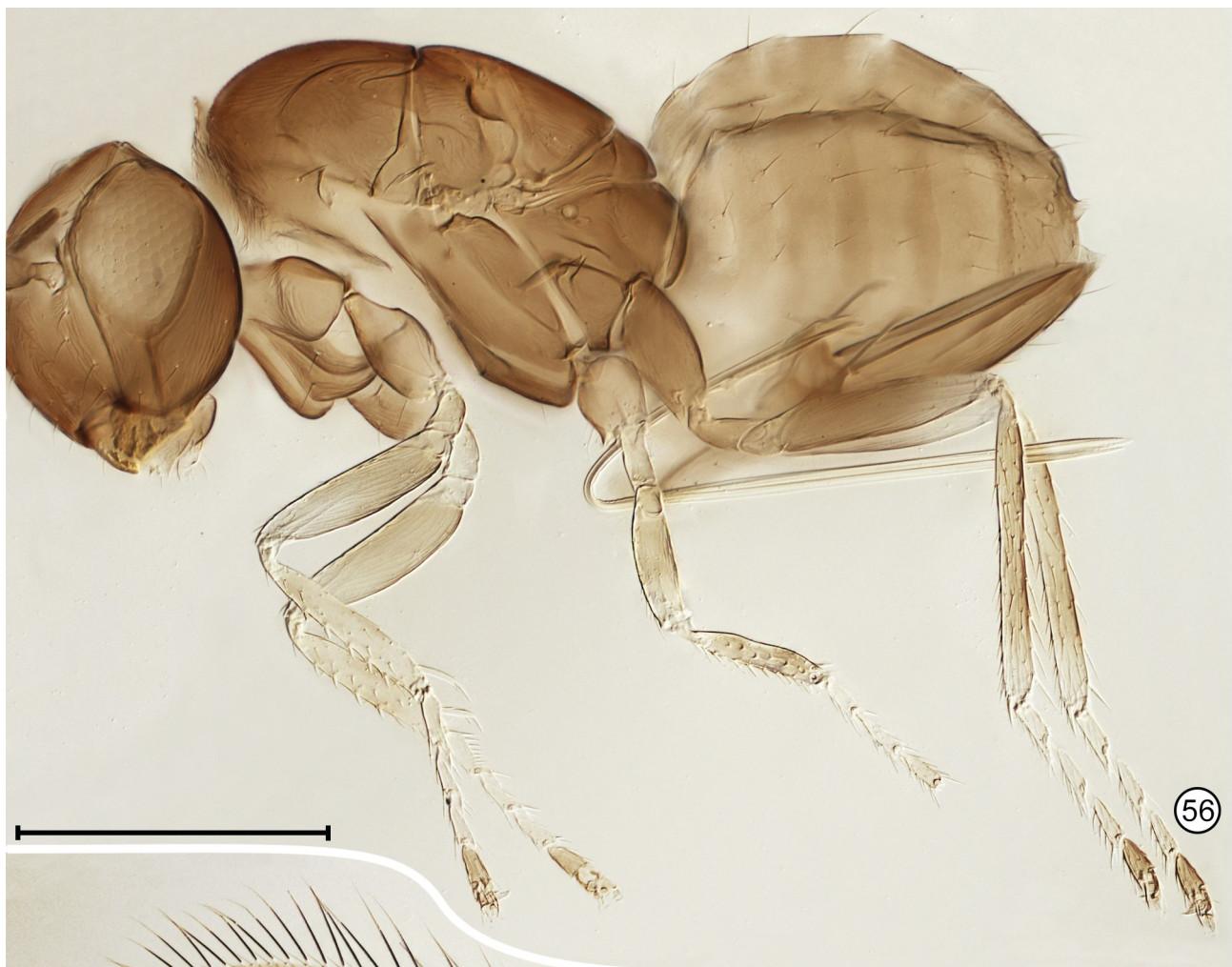
**FIGURES 50, 51.** *Anaphes inexpectatus*, paratype female from Australia, Tasmania, near Hobart, ex. lab. culture in Pretoria, South Africa, i.1989, N.J. van Rensburg, ex. *Gonipterus scutellatus* [misidentification, probably *G. platensis*]. 50, head, lateral; 51, antenna. Scale bars = 100 µm.



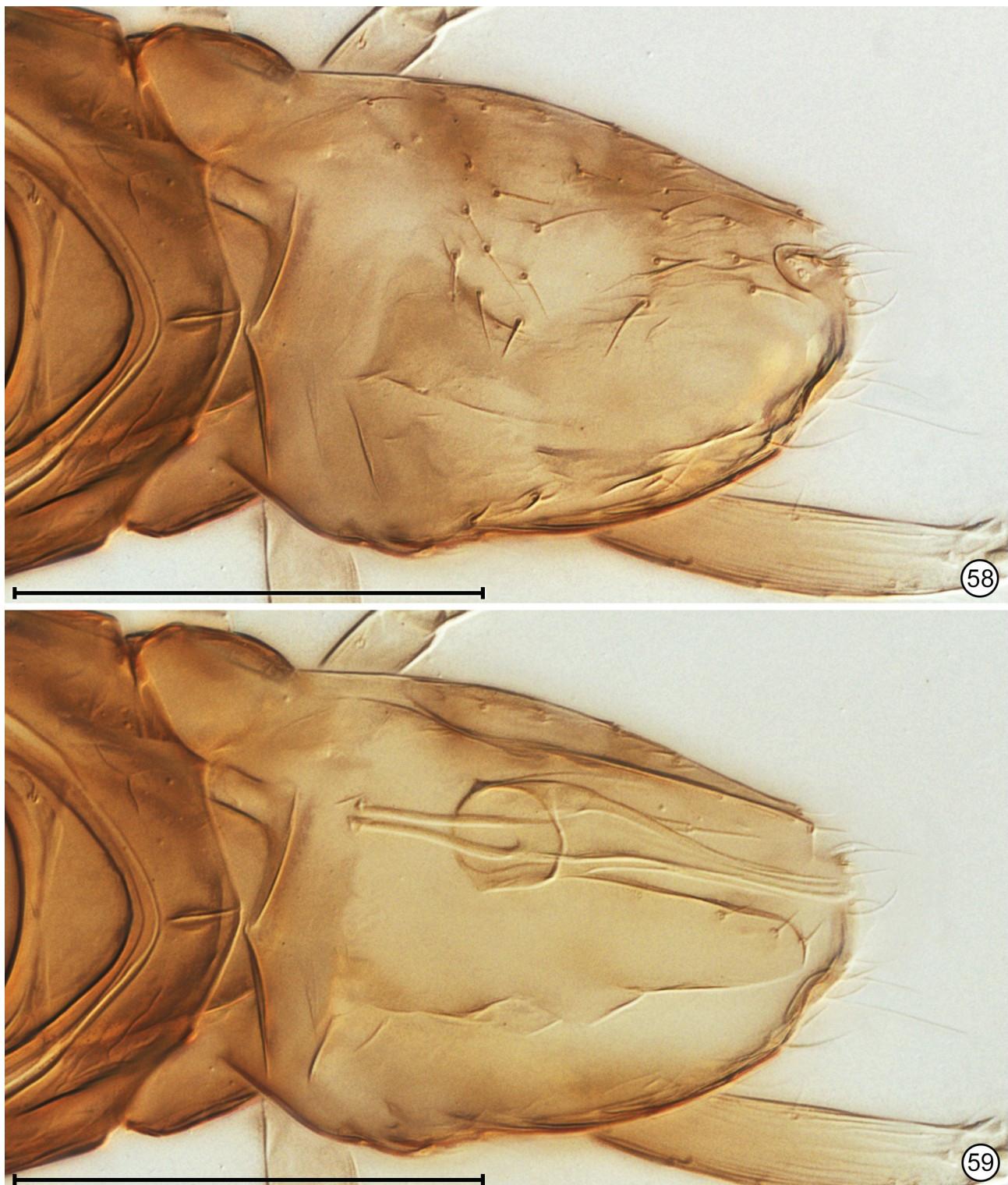
**FIGURES 52, 53.** *Anaphes inexpectatus*, paratype male, same Data as in Figs 50, 51. 52, head + antennae; 53, head, posterior, seen through head from anterior. Scale bars = 100 µm.



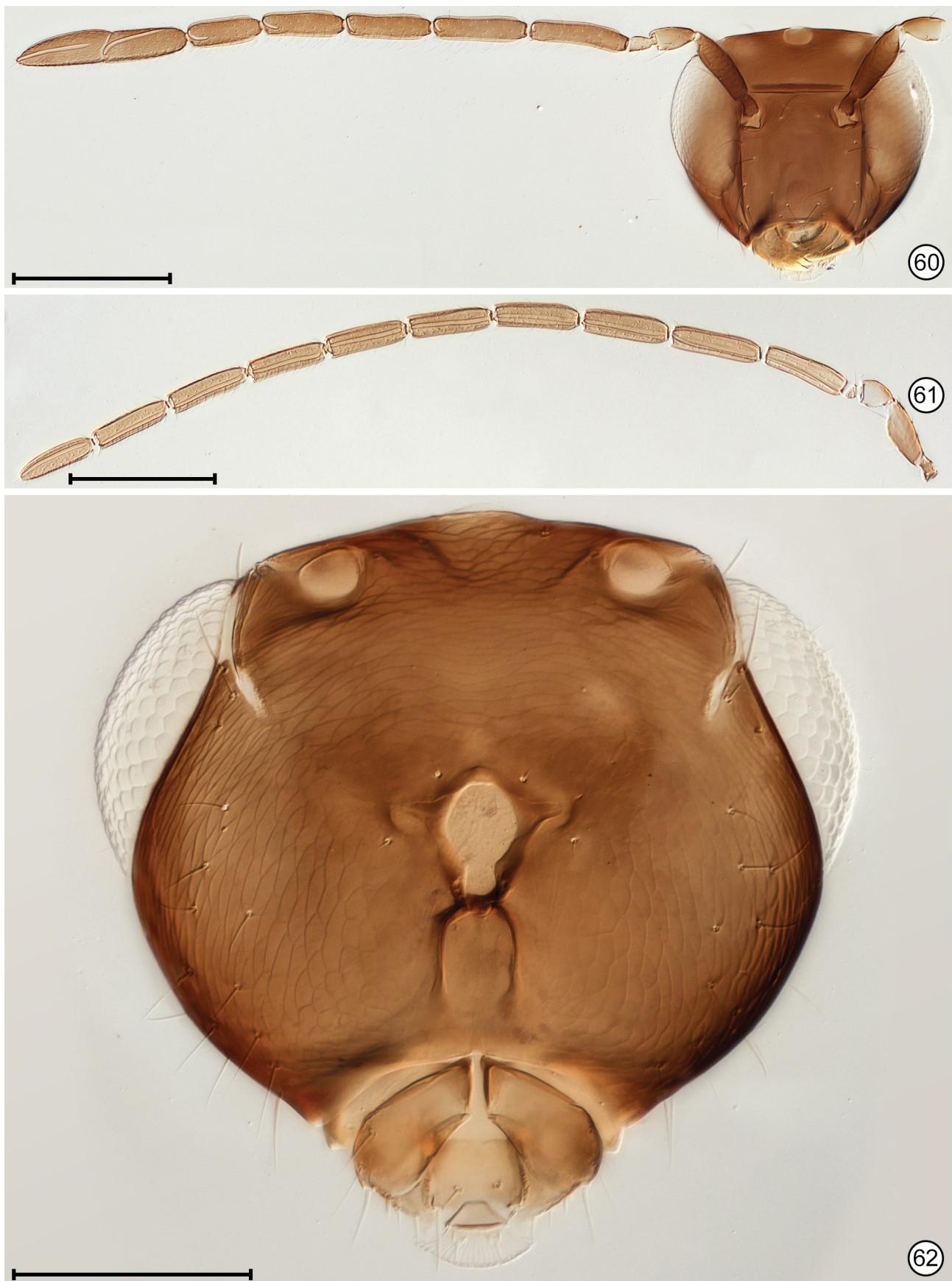
**FIGURES 54, 55.** *Anaphes inexpectatus*, paratype, same data as in Figs 50, 51. 54, male mesosoma, dorsal; 55, female mesosoma, lateral. Scale bars = 100  $\mu\text{m}$ .



**FIGURES 56, 57.** *Anaphes inexpectatus*, paratype female, same data as in Figs 50, 51. 56, habitus, lateral; 57, wings. Scale bars = 200  $\mu\text{m}$ .



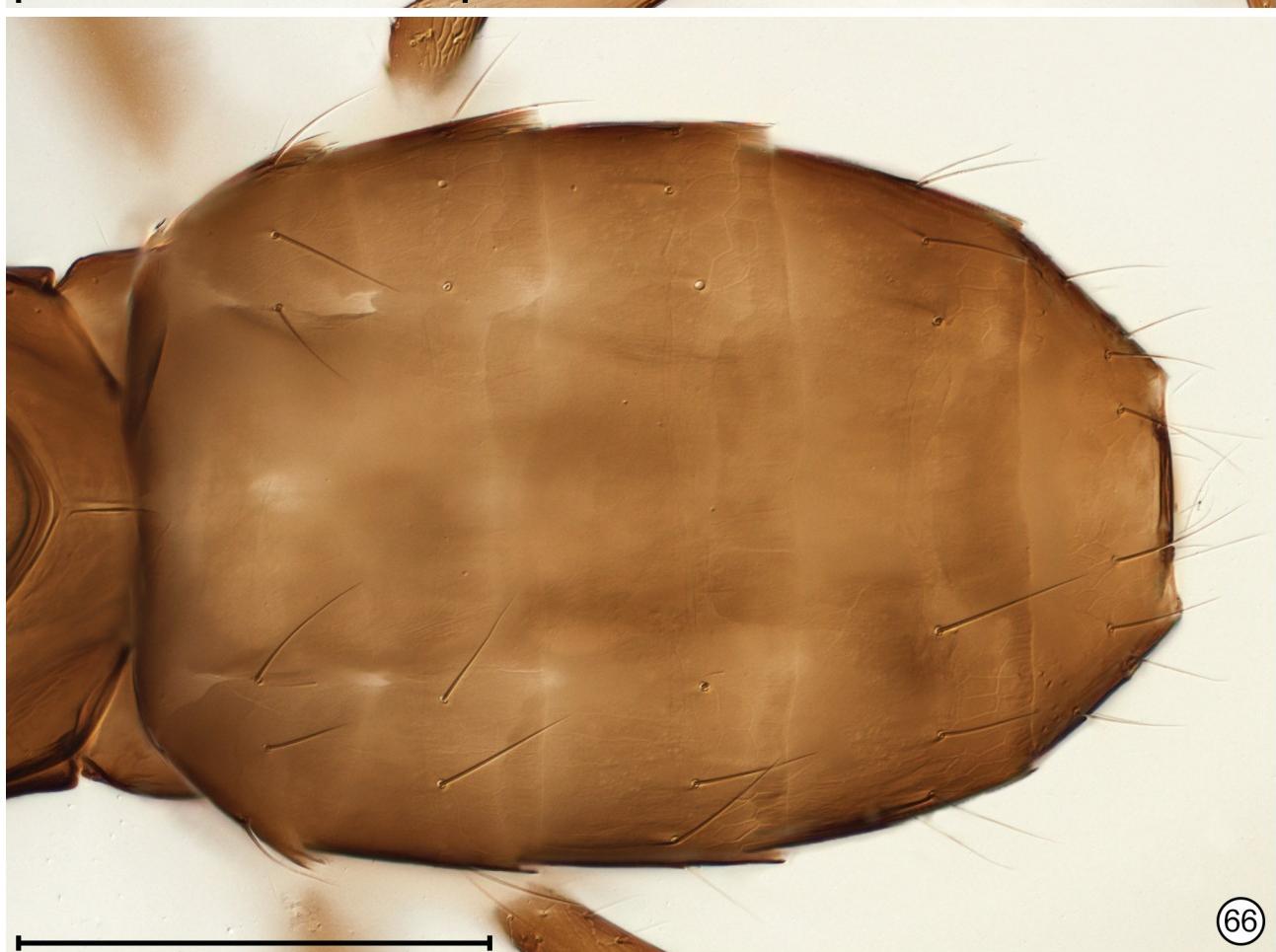
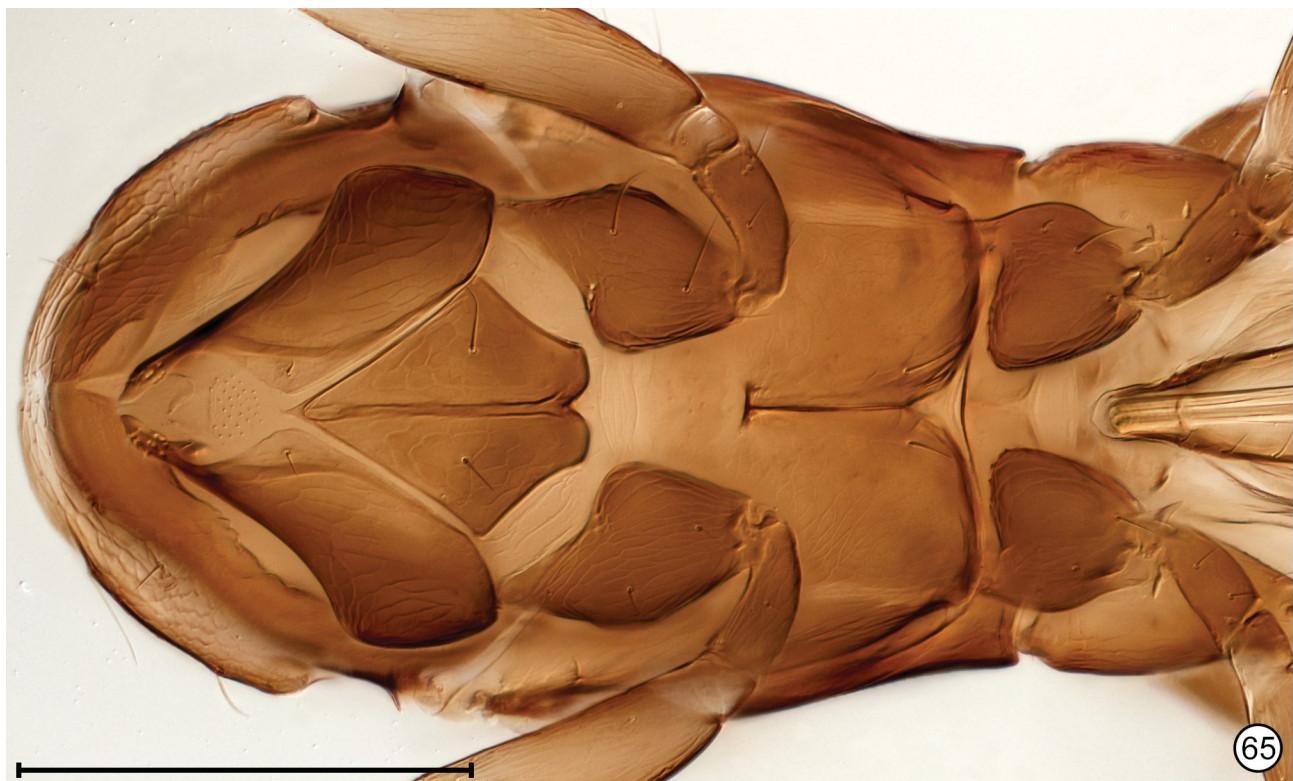
**FIGURES 58, 59.** *Anaphes inexpectatus*, paratype male, same data as in Figs 50, 51. 58, metasoma, dorsal (slightly damaged); 59, mesosoma dorsal, genitalia as seen through mesosoma. Scale bars = 100  $\mu\text{m}$ .



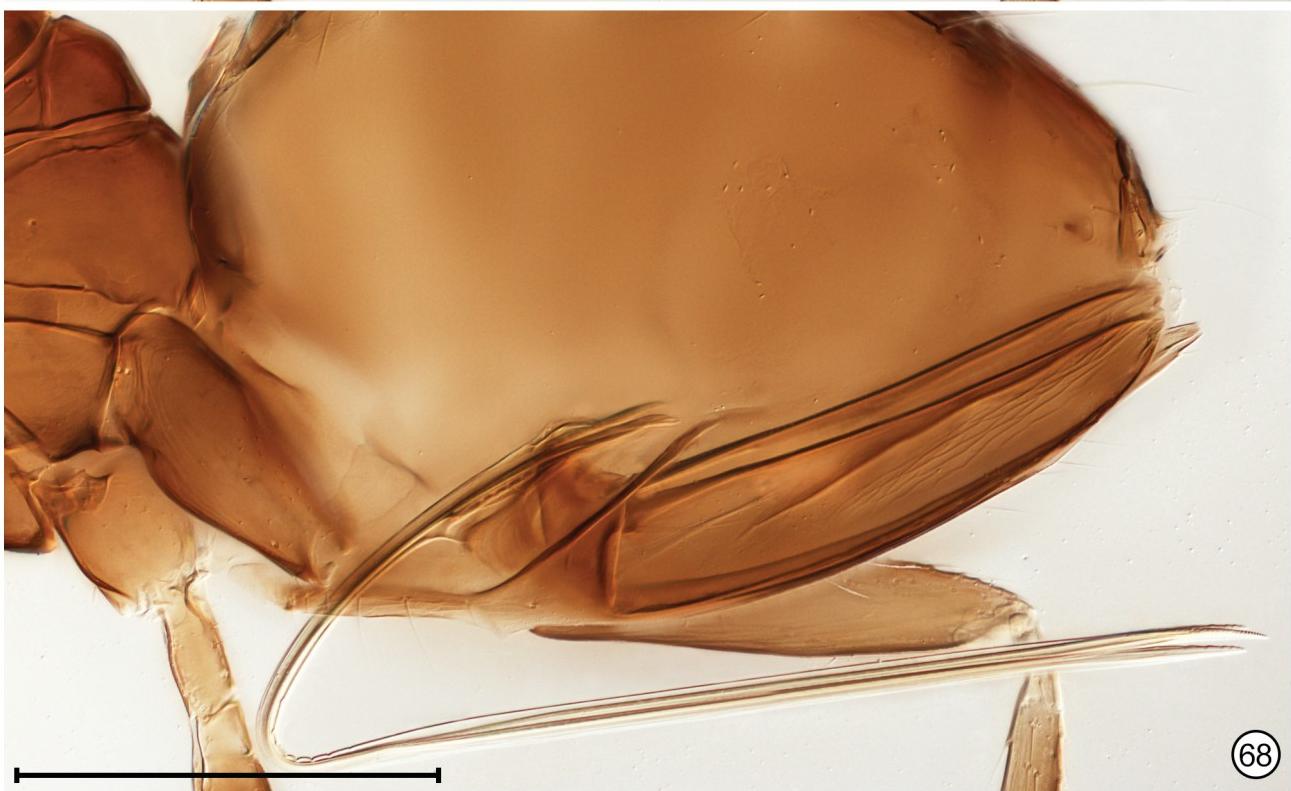
**FIGURES 60–62.** *Anaphes nitens*, specimens from South Africa, Cape Province, Sassveld forestry Station near George, vii.1986, ex *Gonipterus scutellatus*. 60, female, head + antenna, anterior; 61, male antenna; 62, male head, posterior. Scale bars = 200  $\mu\text{m}$ .



**FIGURES 63, 64.** *Anaphes nitens*, female, same Data as in Figs 60–62. 63, mesosoma, dorsal; 64, mesosoma, lateral. Scale bars = 200  $\mu$ m.



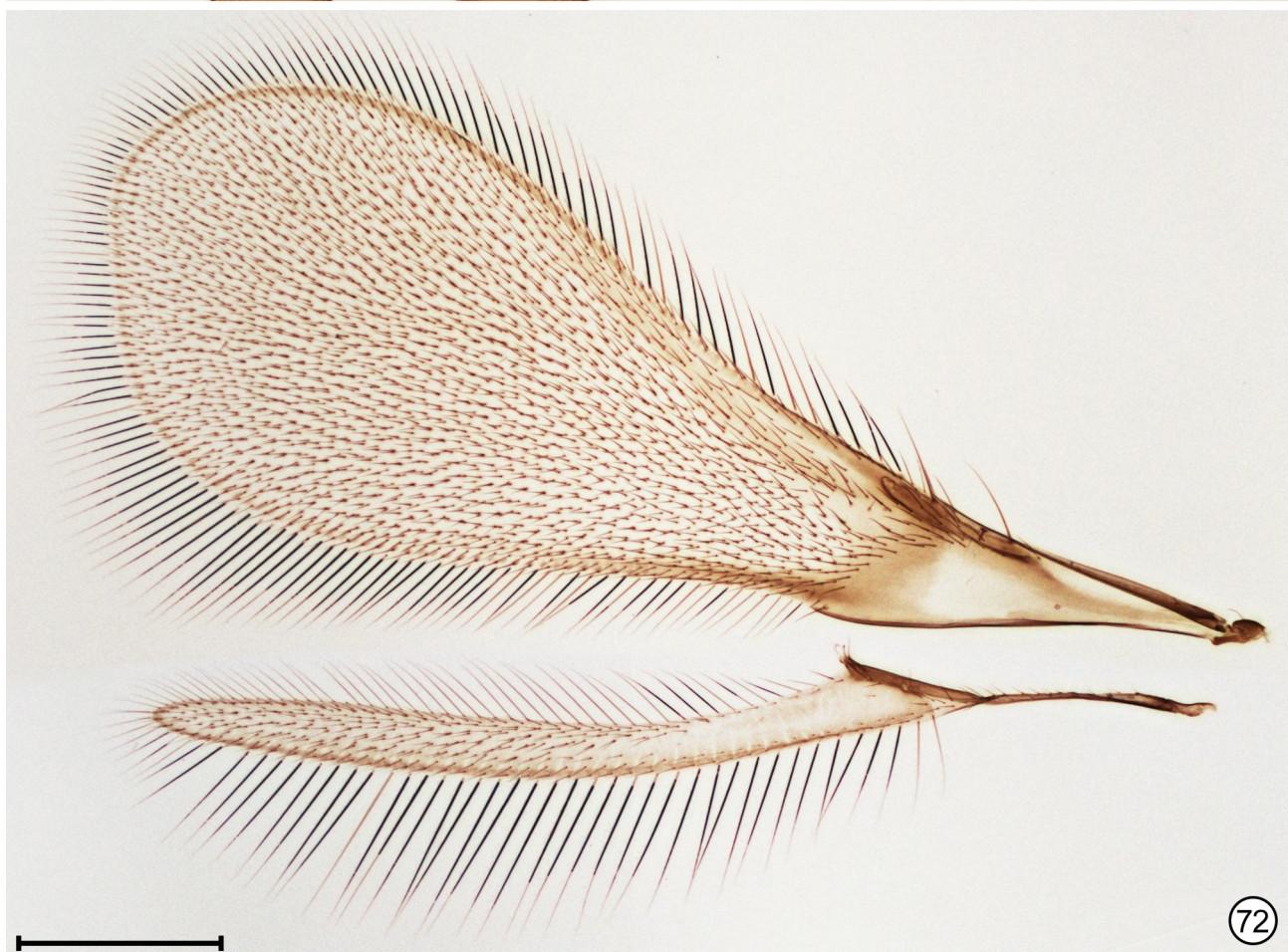
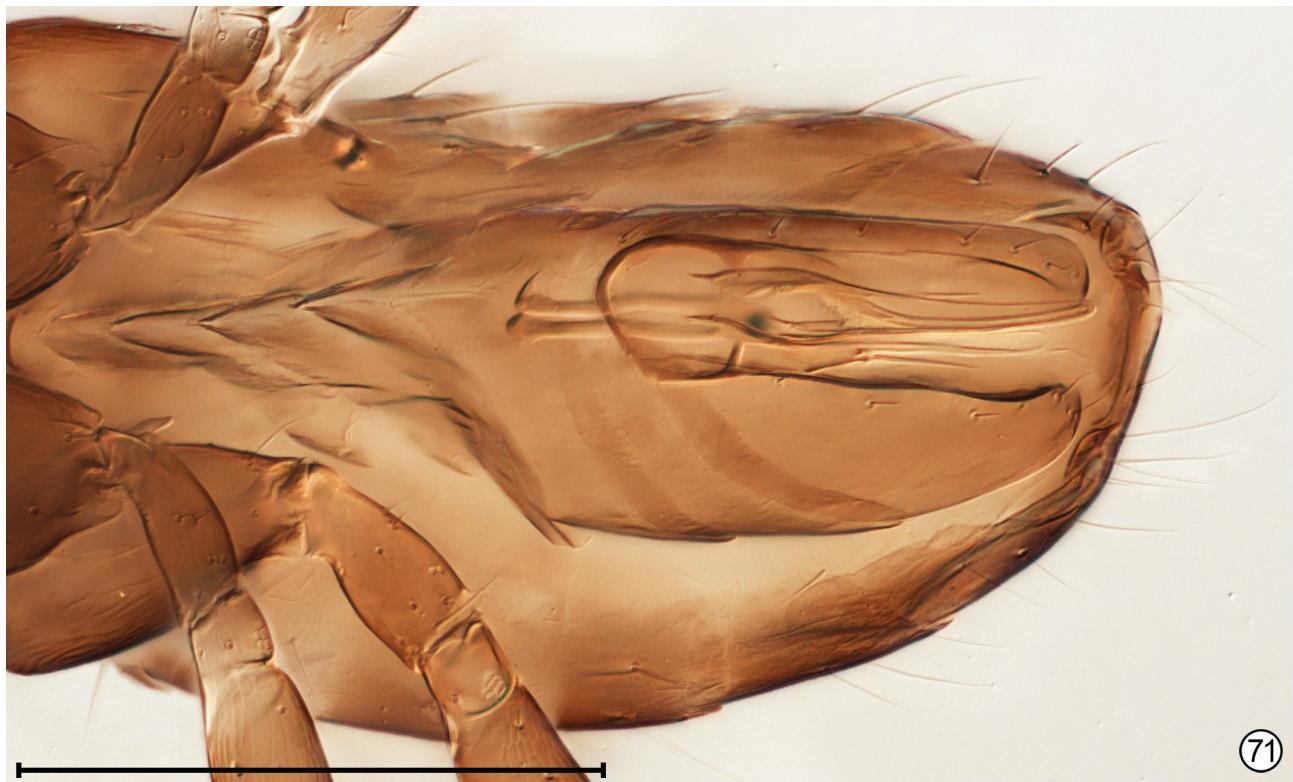
**FIGURES 65, 66.** *Anaphes nitens*, female, same data as in Figs 60–62. 65, mesosoma, ventral; 66, metasoma, dorsal. Scale bars = 200  $\mu$ m.



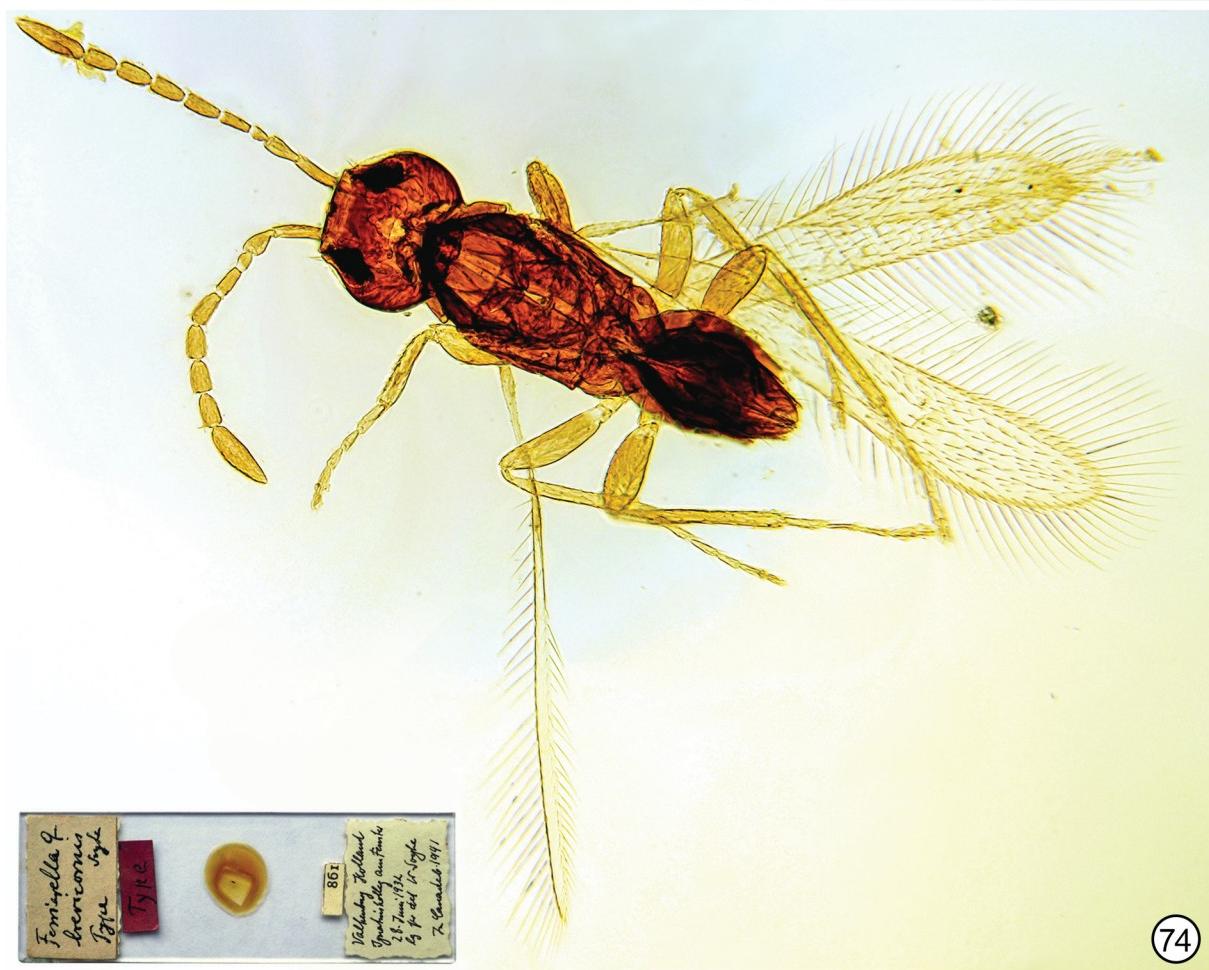
**FIGURES 67, 68.** *Anaphes nitens*, female, same data as in Figs 60–62. 67, metasoma, lateral; 68, metasoma, midsagittal (= median) plane, showing internal structure of genitalia. Scale bars = 200 µm.



**FIGURES 69, 70.** *Anaphes nitens*, female, same data as in Figs 60–62. 69, metasoma, dorsal, genitalia as seen dorsally through body; 70, metasoma, ventral, as seen through body. Scale bars = 200  $\mu\text{m}$ .



**FIGURES 71, 72.** *Anaphes nitens*, male, same data as in Figs 60–62. 71, metasoma, ventral, as seen dorsally through body; 72, wings. Scale bars = 200 µm.



**FIGURES 73, 74.** *Anaphes* spp., habitus and type slide (body length cited from original description). 73, *arenbergi* (0.699 mm); 74, *brevicornis* (0.594 mm).



**FIGURES 75, 76.** *Anaphes* spp., habitus and type slide (body length cited from original description). 75, *crassipennis* (0.82 mm); 76, *ensipennis* (0.72 mm).

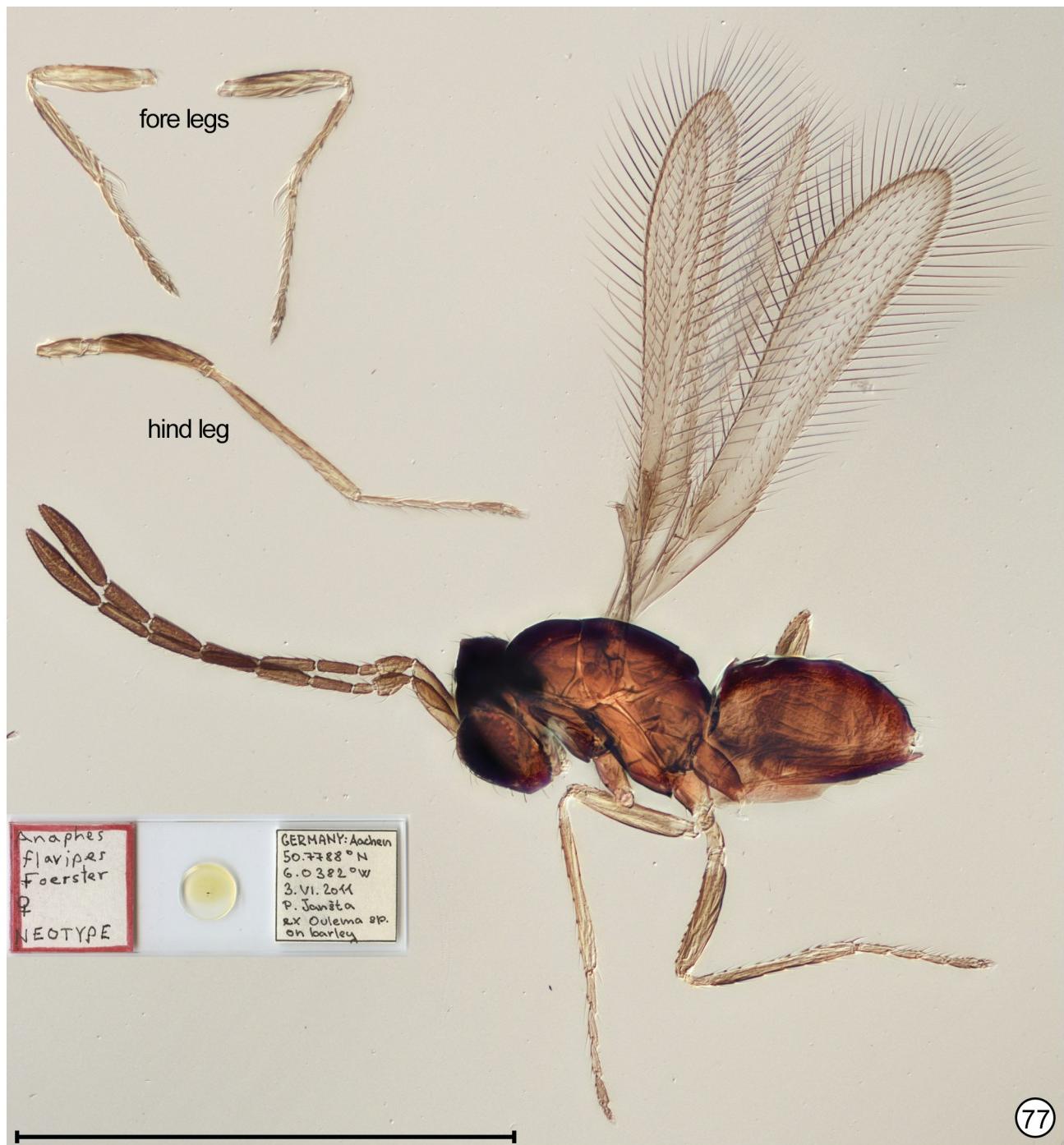


FIGURE 77. *Anaphes flavipes*, habitus and neotype slide. Scale bar = 500 µm.



**FIGURE 78.** *Anaphes fuscipennis*, lectotype habitus (body length cited from original description = 0.025 inches [= 0.635 mm]).



**FIGURE 79.** *Anaphes fuscipennis*, habitus (specimen faded to brown), Canada, Nova Scotia, Sydney,  $46^{\circ}08.712'N$   $60^{\circ}10.962'W$ , 14.vi.2004, sweeping fallow field, H. Goulet, C. Boudreault, A. Badiss. Scale bar = 500  $\mu$ m.



**FIGURES 80, 81.** *Anaphes* spp., habitus and type slide (body length cited from original description). 80, *gauthieri* (0.473 mm); 81, *medius* (0.83 mm).



**FIGURE 82.** *Anaphes globosicornis*, habitus. 82a, body without head; 82b, head + antennae and type slide. Body length cited from original description = 0.63 mm.



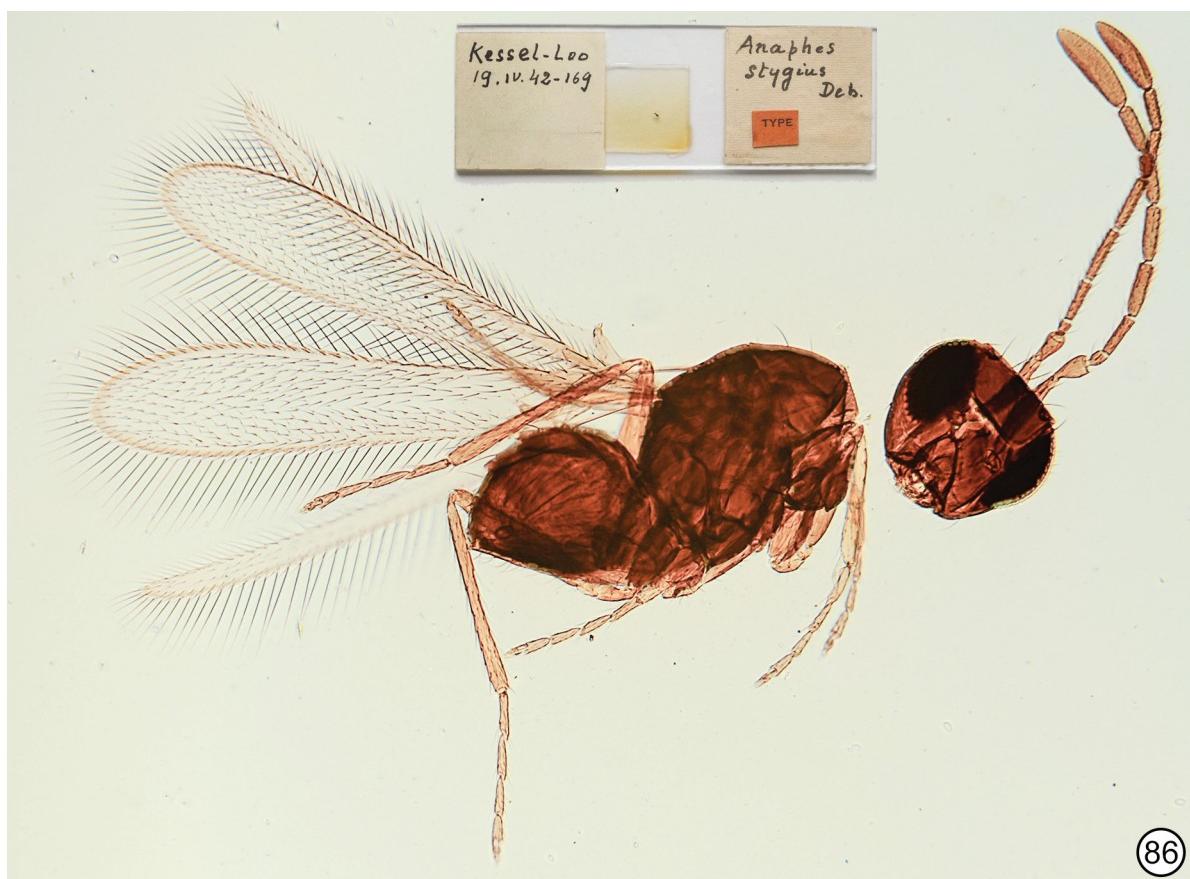
**FIGURES 83, 84.** *Anaphes* spp., habitus and type slide (body length cited from original description). 83, *ovipositor* (0.39 mm); 84, *quadraticornis* (0.60 mm).

Anaphes  
regulus Walker  
LECTOTYPE: ♀  
M.de V.Graham  
det. 1972

28.



FIGURE 85. *Anaphes regulus*, lectotype, habitus (0.47 mm—mesosoma + metasoma only, cited from Graham [1982]).



**FIGURES 86, 87.** *Anaphes* spp., habitus and type slide (body length cited from original description). 86, *stygius* (0.706 mm); 87, *wolfsthali* (0.75 mm).



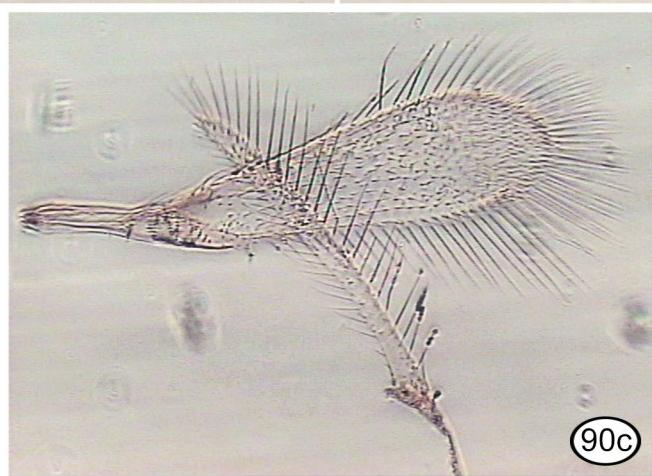
**FIGURES 88, 89.** *Anaphes* spp., habitus and type slide (body length cited from original description). 88, *angustipennis* (0.431 mm); 89, *crassus* (0.63 mm).



90a



90b

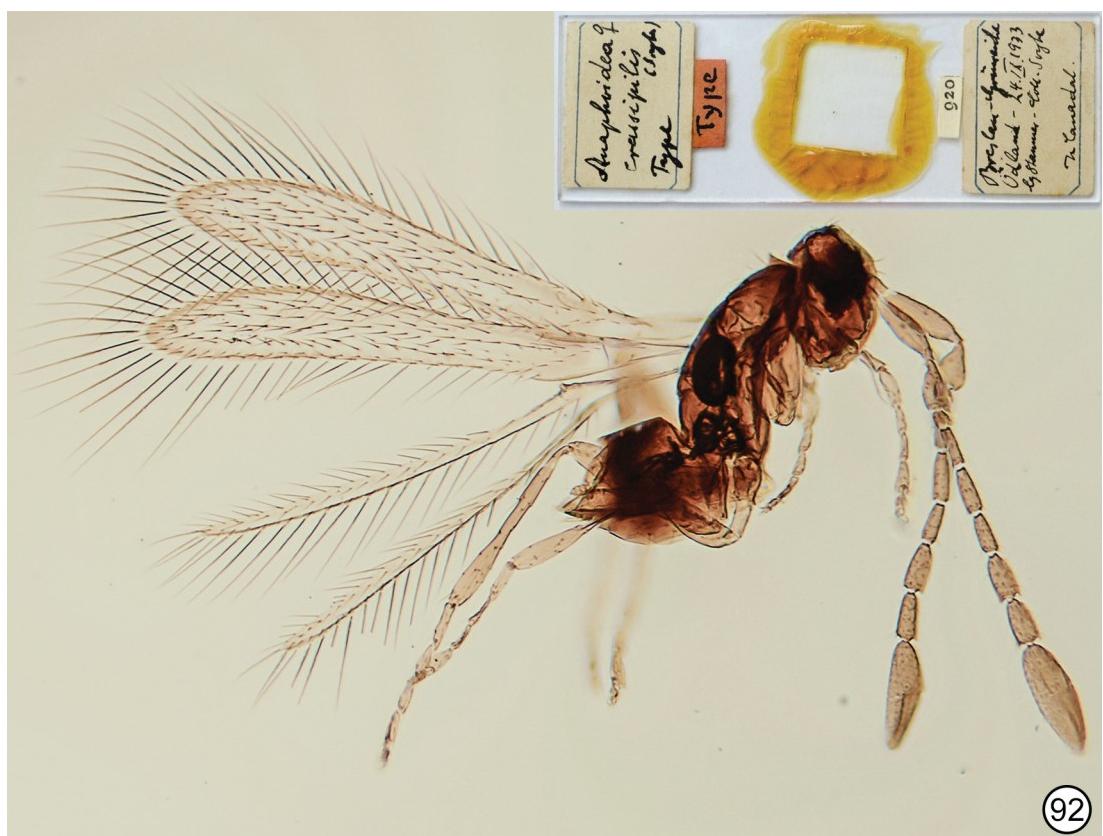


90c

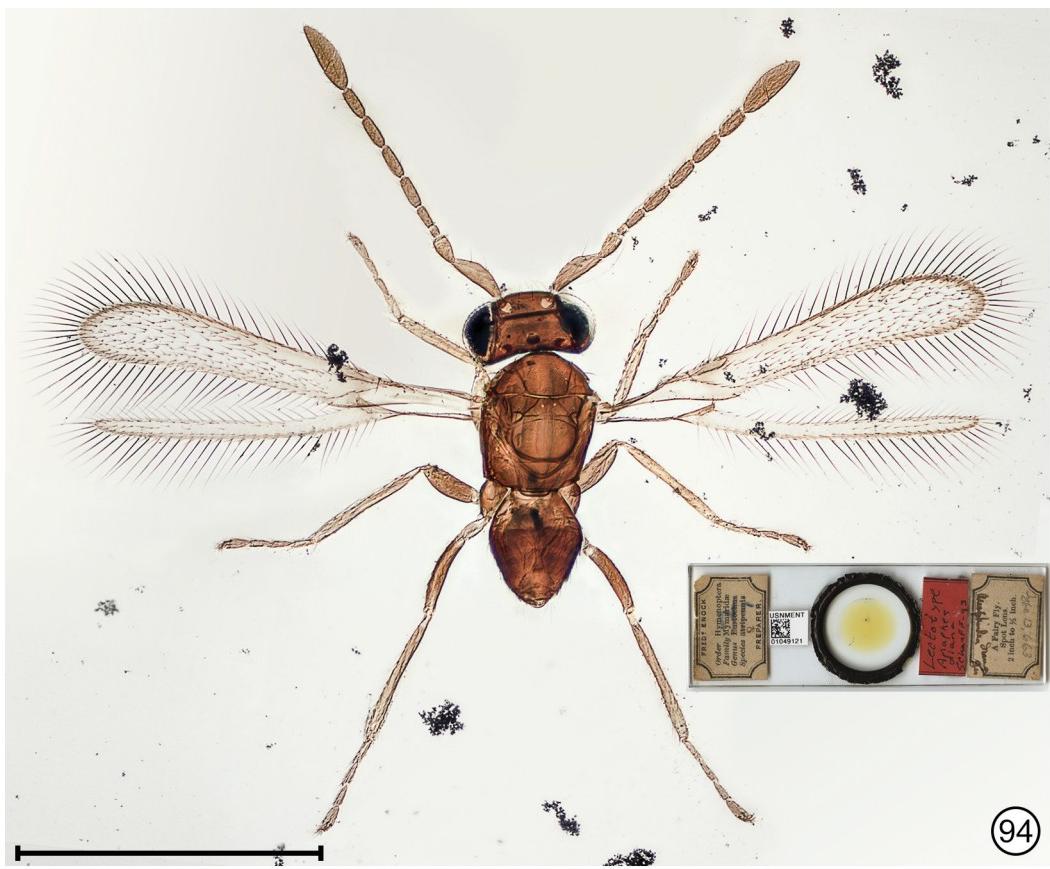
**FIGURE 90.** *Anaphes collinus*, lectotype. 90a, habitus (0.4 mm, cited from Graham's [1982] description); 90b, antenna; 90c, wings.



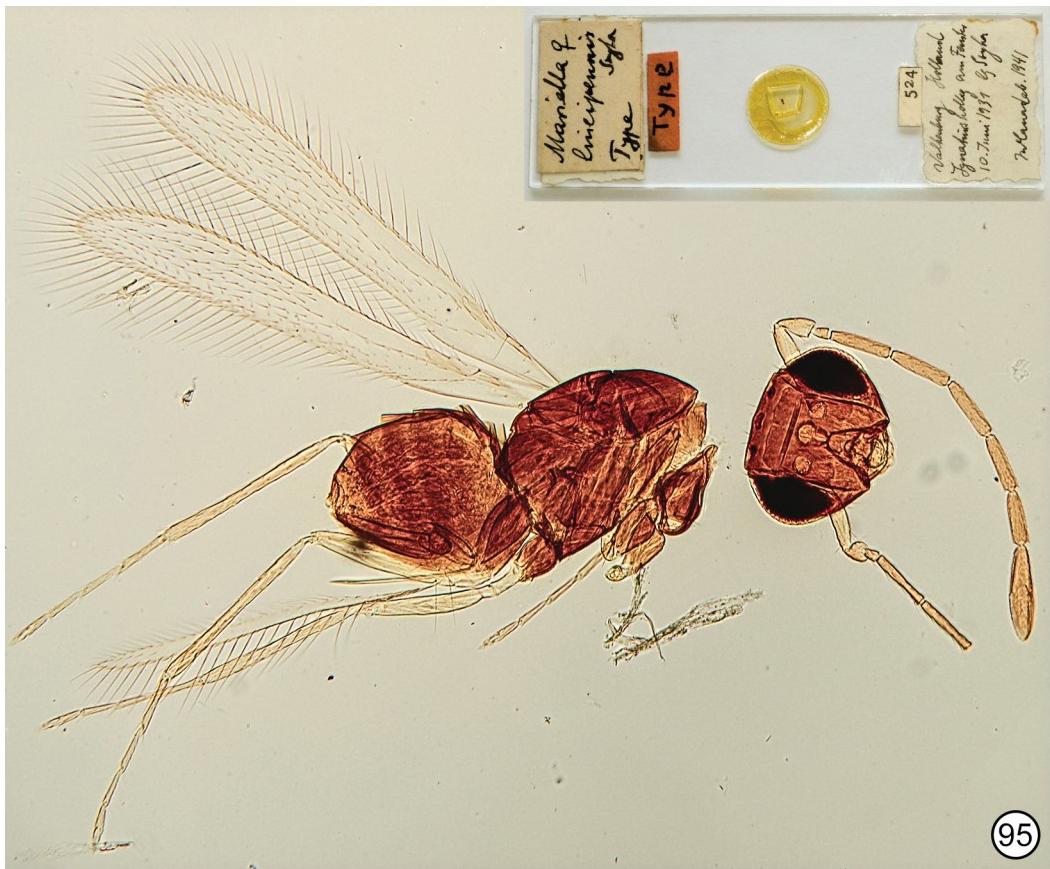
**FIGURE 91.** *Anaphes crassicornis*, lectotype, habitus ( $\approx 0.4$  mm, cited from Graham's [1982] description). Scale bar = 500  $\mu\text{m}$ .



**FIGURES 92, 93.** *Anaphes* spp., habitus and type slide (body length cited from original description). 92, *crassipilis* (0.36 mm); 93, *debilipennis* (0.54 mm).



(94)



(95)

**FIGURES 94, 95.** *Anaphes* spp., habitus and type slide. 94, *diana*; 95, *lineipennis* (0.63 mm, body length cited from original description). Scale bar for 94 = 500 µm.



96a



96b



97

**FIGURES 96, 97.** *Anaphes longicornis*, habitus. 96a, lectotype (0.75 mm, cited from Graham's (1982) description); 96b, lectotype, antenna; 97, paralectotype, male.



98



99

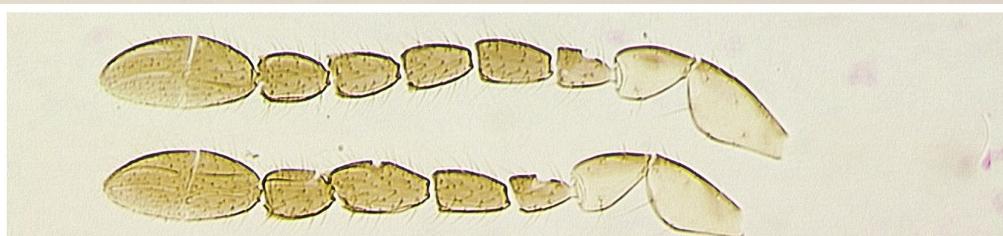
**FIGURES 98, 99.** *Anaphes* spp., habitus and type slide (body length cited from original description). 98, *luna*; 99, *maiialis* (0.595 mm). Scale bar for 98 = 500 µm.



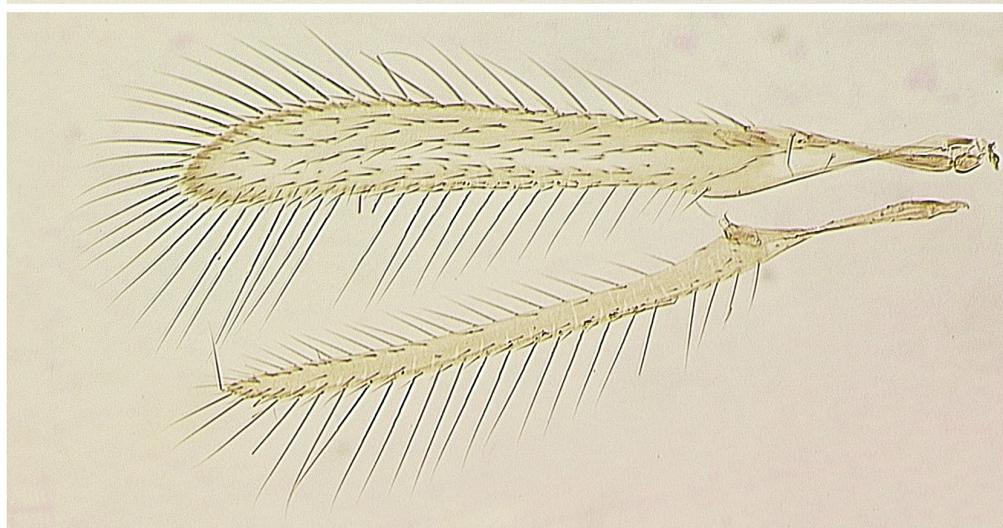
**FIGURES 100, 101.** *Anaphes* spp., habitus and type slide (body length cited from original description). 100, *parallelipennis* (0.612 mm); 101, *silesicus* (0.43 mm).



(102)



(103)



(104)

**FIGURE 102–104.** *Anaphes* sp., teratological specimen from Greece, Central Macedonia, Lake Kerkini 41°08'15.6"N 23°13'01.2"E, 65 m, 23–29.v.2006, G. Ramel (UCRC); 102, dorsal habitus, note apparently 3-segmented tarsi, enlarged in insets; 103, antennae, both with  $fl_1 + fl_2$  fused and one (lower image) also with  $fl_4 + fl_5$  fused; 104, wings. Fore wing length 585  $\mu\text{m}$ , antennae length from apex of clava to base of pedicel 320  $\mu\text{m}$  (4-segmented funicle) and 344  $\mu\text{m}$  (5-segmented funicle). Body length ca. 0.58 mm.